
Seasonal patterns in phytoplankton biomass in coastal ecosystems

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Abstract. We test, through a compilation of published data, whether specific trends in phytoplankton biomass seasonality can be generalized in northern temperate enclosed coastal ecosystems (ECE) and northern temperate open coastal ecosystems (OCE). Bimodal cycles (i.e. displaying two annual peaks) are the most frequent trends in both ecosystems, and whereas they mostly peaked at late winter and fall in OCE, they mostly peaked in spring and late summer, and also over a wider range of months, in ECE. The interaction between restricted depth or tidal stirring and light seasonality in ECE may be responsible for these differences. Moreover, bimodal cycles reached higher biomass peaks in ECE, which can result from higher water column nutrient concentrations. Unimodal cycles (one annual peak) also occurred commonly in both ecosystems, and whereas they peaked throughout winter and spring in OCE, they peaked mostly in summer in ECE. We suggest that the high nutrient concentrations typically found in ECE waters can alleviate nutrient limitation of phytoplankton growth and couple phytoplankton growth with light and stratification seasonality. These results reveal broad-scale patterns in phytoplankton seasonality in temperate coastal ecosystems, and help identify physical processes generating these patterns.

Introduction

Temporal oscillations of phytoplankton biomass are often very variable. The number, timing and magnitude of annual blooms may differ remarkably among close locations (Vives and López-Benito, 1957; Patten *et al.*, 1963; Stockner *et al.*, 1977) and among years within the same location (Motoda *et al.*, 1987; Uhlig and Sahling, 1990; Harris *et al.*, 1991). General seasonal trends of phytoplankton biomass have been firmly characterized only in few oceanic and coastal regions (Sinclair *et al.*, 1981; Evans and Parslow, 1985; Banse and English, 1994; Longhurst, 1995). Moreover, recent reviews (Yoder *et al.*, 1993; Banse and English, 1994) show that certain seasonal trends thought to occur in many offshore regions are not so pervasive. For instance, the spring bloom in the temperate North Atlantic, regarded as typical by many authors (confer Colebrook, 1979), does not seem such a prevalent phenomenon (Banse and English, 1994). Hence, the question whether broad-scale seasonal trends in phytoplankton biomass can be established needs clarification.

Elucidating broad-scale seasonal patterns in phytoplankton biomass is of interest because it can help reveal general controls of phytoplankton temporal dynamics. The association between broad-scale seasonal patterns and prevalent driving factors has been investigated mostly in oceanic regions. For instance, Banse (1987) characterizes a distinct seasonal trend throughout most of the Arabian Sea, and assigns it to the monsoon regime. Similarly, Banse and English (1994) attribute different seasonal patterns in oceanic regions to differences in temperature maxima and nutrient concentrations. Contrastingly, few physical factors responsible for broad-scale phytoplankton seasonality have been identified in coastal regions. This may be due to the fact that coastal environments differ

remarkably in their physical and hydrographic properties, such as depth, tidal stirring or nutrient loadings, and these differences can lead to complex, contrasting phytoplankton dynamics among them (Cloern, 1996).

Two types of ecosystems can be differentiated in coastal environments on the basis of physical and hydrographic properties (Cloern, 1996): enclosed coastal ecosystems (ECE) and open coastal ecosystems (OCE). ECE represent sheltered regions at the transition between land and OCE, such as tidal rivers, estuaries, coastal lagoons and embayments. ECE often have restricted depth, and are frequently subject to variable riverine freshwater inputs and tidal stirring. In temperate ECE, the effects of light and water stratification on phytoplankton growth (Colebrook, 1979; Harris, 1986) may interact with the effects of freshwater inputs, tidal stirring and restricted depth. Freshwater run-off may entail positive [i.e. high nutrient concentrations (Justic *et al.*, 1995; Nixon, 1995) or promoted physical stability under fresh-sea water convergence (Simpson *et al.*, 1991)] or negative [i.e. turbidity (Cloern, 1987) or washing off by advection (Delesalle and Sournia, 1992; Pace *et al.*, 1992)] effects on phytoplankton growth. Furthermore, tidal oscillations can generate substantial turbulence in ECE, thereby restricting phytoplanktonic growth (Cloern, 1991; Monbet, 1992). Finally, restricted depth in ECE commonly generates substantial water column turbidity which may be an important control of phytoplankton dynamics (Cloern, 1987). Therefore, if seasonal trends of phytoplankton biomass can indeed be generalized in temperate coastal environments, it can be expected that (i) temperate ECE and temperate OCE show different seasonal trends, and that (ii) physical characteristics of ECE, such as restricted depth, substantial tidal stirring and high nutrient concentrations, are responsible for these differences.

In this report, we compile published results to define general seasonal trends in phytoplankton biomass in northern temperate ECE and OCE. In particular, we establish patterns in the number, timing and magnitude of annual biomass peaks. We then test whether differences in these patterns between ECE and OCE can be attributed to differences in physical and hydrological factors, such as restricted depth, tidal range and high nutrient concentrations.

Method

We searched published reports of time series of phytoplankton biomass in northern temperate ECE and OCE (comprised within 25–65°N, nearly all of them within 30–50°N; Table I) covering at least 1 year. Mean chlorophyll concentration within the euphotic layer (mg chlorophyll m⁻³) was used as a proxy for phytoplankton biomass. Whenever concentration values were not provided directly in the reports, they were derived as the product between the abundance of phytoplanktonic cells and corresponding cell chlorophyll contents (Parsons, 1961; Eppley, 1972; Ray *et al.*, 1989). All reports compiled allowed monthly resolution of phytoplankton temporal dynamics (Table I). In each report, the number, month and magnitude of biomass peaks per annual cycle were recorded as explicitly stated by the authors. If several stations and/or years were covered within a given ECE or OCE, the number, month and magnitude of annual peaks were averaged

among the stations and/or years. Whenever provided in the reports, we also recorded mean depth, mean tidal range and the yearly ranges in nitrate (NO_3) and inorganic phosphorus (PO_4) concentrations (mg l^{-1}) in the water column.

The number and timing of peaks detected in time series of phytoplankton biomass largely depend on the sampling frequency employed (Harris, 1984; Legendre, 1990). Although sampling frequency ranged considerably among the reports compiled (Table I), the ECE compiled did not show a different sampling frequency from the OCE compiled (ANOVA, $P > 0.05$). Hence, differences in number and timing of annual biomass peaks between these two types of ecosystem cannot be influenced by differences in sampling frequency. Moreover, phytoplankton dynamics within a given location may show substantial inter-annual variability (Pilson, 1985; Motoda *et al.*, 1987) and, because most reports compiled only covered 1 year, this interannual variability could affect the comparison of phytoplankton dynamics between ECE and OCE. Yet, the ECE and OCE compiled with sampling periods longer than 1 year showed little inter-annual variability in the number and timing of annual biomass peaks (Table II). This fact, along with the high number of ECE and OCE compared (Table I), support that interannual variability in phytoplankton biomass should not affect the differences found in number and timing of annual biomass peaks between ECE and OCE, even though some of the sites compiled, such as Narragansett Bay (Pilson, 1985), may show substantial interannual variability.

Differences in the number of biomass peaks per annual cycle between ECE and OCE were tested with ANOVA. Differences in the timing of peak biomass between ECE and OCE were examined by comparing the histograms of the month of peak biomass with the χ^2 statistic (Zar, 1984). Months with an extremely low frequency both in ECE and OCE were pooled or removed from the analyses to meet the assumptions of this test (Cochran, 1954). Variance in the timing of peak biomass was measured with the Shannon diversity index of the month of peak biomass (H' ; Zar, 1984), and differences in diversity between ECE and OCE were analysed with the t statistic (Hutcheson, 1970). Differences in the magnitude of biomass peaks between ECE and OCE were tested by the non-parametric Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1995) to cope with the marked non-normality and heteroscedasticity of this variable. Differences in nutrient concentrations between ECE and OCE were analysed with ANOVA. The association between timing of peak biomass and depth and tidal range in ECE and OCE was examined with least-square regression techniques. Data were tested for the requirements of ANOVA and least-square regression techniques and log transformed if necessary.

Results

Temperate ECE and OCE did not differ in the number of biomass peaks per annual cycle (Table I; ANOVA, $P > 0.05$). About 65% of the ECE and OCE compiled featured two peaks per annual cycle (i.e. bimodal cycles), with the rest of the ecosystems of either type showing one peak (i.e. unimodal cycles).

Unimodal cycles peaked mostly in summer in temperate ECE and throughout

Table 1. Data set compiled. Values separated by a comma are relative to the first and second biomass peaks, respectively, in ecosystems with bimodal cycles (n.a., not available)

Type of system	Reference	Location	Sampling frequency	Number of biomass peaks per annual cycle	Months of biomass peak	Magnitude of biomass peaks (mg Chl m ⁻³)	Annual NO ₃ range (mg l ⁻¹)	Annual PO ₄ range (mg l ⁻¹)	Mean depth (m)	Mean tidal range (m)
ECE	Sakshaug and Mýklestad, 1973	Trondheims Fjord (Norway)	Weekly	2	April, September	14.5, 3.5	n.a.-0.37	0.0096-0.086	525	1.83
	Williams and Murdoch, 1966	Beaufort Channel (USA)	Biweekly	1	March	8			1.1	0.8
	Welch <i>et al.</i> , 1972	Duwamish Estuary (USA)	Biweekly	1	August	52.5			6.4	1.5
	Patten <i>et al.</i> , 1963	Lower Chesapeake Bay (USA)	Biweekly	1	April, September	13.9, 10		0-0.18	7.1	0.7
	Elmer, 1970	Upper Chesapeake Bay (USA)	Biweekly	1	September	44			7	0.7
	Carpenter, 1971	Fear River Estuary (USA)	Monthly	1	June	7			10	1.4
	Thayer, 1971	Newport Estuary (USA)	Monthly	1	May, July	9.5, 7		0.0061-0.081	7	0.8
	Takahashi <i>et al.</i> , 1977	Saanich Inlet (Canada)	Weekly	2	May, October	22, 9		0.012-1.48	100	
	Vives and López-Bonito, 1957	Ría de Vigo (Spain)	Biweekly	2	May, September	22.1, 12.5		0.001-0.01	33.3	2.5
	Stockner <i>et al.</i> , 1977	Howe Sound (Canada)	Monthly	2	April, September	4.7, 1.4		0.015-0.08	221.4	3.2
	Cadée and Hegeman, 1974a	Western Wadden Sea (The Netherlands)	Monthly	2	April, June	27.13			6.7	2.3
	Cadée and Hegeman, 1974a	Central Wadden Sea (The Netherlands)	Monthly	2	April, August	20.16			6.7	2.3
	Cadée and Hegeman, 1974a	Eems Estuary (The Netherlands)	Monthly	2	May, August	14.10			6.7	2.3
	Cadée and Hegeman, 1974a	Dollard Estuary (The Netherlands)	Monthly	2	June, September	17.14			6.7	2.3
	Roman <i>et al.</i> , 1983	Isselmer Estuary (The Netherlands)	Monthly	2	April, September	45, 45			6.7	2.3
	Lively <i>et al.</i> , 1983	Biscayne Bay (USA)	Monthly	1	January, May	0.7, 4.8		0.015-0.05	2	0.5
	Short and Mathieson, 1992	Great South Bay (USA)	Monthly	1	August	23		0.006-0.06	2	0.25
	Mouniford, 1984	Great Bay Estuary (USA)	Monthly	2	April, August	6.5, 6		0.0096-0.48	2.7	2.1
	Tett and Wallis, 1978	Barnegat Bay (USA)	Biweekly	1	February, July	23, 20		0.0062-2.48	1.5	0.6
	Mandelli <i>et al.</i> , 1970	Loch Crean (UK)	Biweekly	1	March	24		0.0062-0.25	18	2.3
	Mallin <i>et al.</i> , 1991	Nassau Bay (USA)	Monthly	1	August	65		0.03-0.19	4.5	0.25
	Taylor and Saloman, 1968	Neuse River Estuary (USA)	Monthly	2	March, September	23, 19		0.001-0.11		
	Taylor and Saloman, 1968	Old Tampa Bay (USA)	Monthly	2	May, September	4.5, 8.9				
	Taylor and Saloman, 1968	Hillsborough Bay (USA)	Monthly	3	January, March, August	12, 13.7, 30.9				
	Taylor and Saloman, 1968	Tampa Bay (USA)	Monthly	2	April, September	8.7, 11.4			1.8	
	Taylor and Saloman, 1968	Tampa Bay-Entrance (USA)	Monthly	2	February, October	3.1, 10.1			30	8
	Taylor and Saloman, 1968	Boca Ciega Bay (USA)	Monthly	2	March, September	11.1, 8.1			35	1.3
	Villate, 1991	Bay of Biscay (Spain)	Monthly	1	August	3			106.5	
	Birrien <i>et al.</i> , 1991	Iroise Sea (France)	Monthly	1	August	4.3		0.012-0.62	6.7	2.3
	Harrison and Platt, 1980	Bedford Basin (Canada)	Biweekly	1	March, September	22, 10		0.0003-0.59	12	
	Bollens <i>et al.</i> , 1992	Dabob Bay (USA)	Monthly	2	April, October	38, 25		0.06-0.29	6.7	2.3
	Admiral <i>et al.</i> , 1985	Eastern Wadden Sea (The Netherlands)	Biweekly	1	May, August	7		0.14-0.48	12	
	Malone, 1977	Hudson River Estuary (USA)	Monthly	1	July	18, 45, 20			5	2.4
	Kilfe and Purdie, 1993	Test Estuary (UK)	Monthly	3	May, June, July	110, 85				
	Moon and Dunstan, 1990	James River Estuary (USA)	Monthly	2	August, September					

Table 1. continued

Type of system	Reference	Location	Sampling frequency	Number of biomass peaks per annual cycle	Months of biomass peak	Magnitude of biomass peaks (mg Chl m ⁻³)	Annual NO ₃ range (mg l ⁻¹)	Annual PO ₄ range (mg l ⁻¹)	Mean depth (m)	Mean tidal range (m)
	Wafar <i>et al.</i> , 1989	Morlaix Estuary (France)	Monthly	1	July	15	0.49–9.3	0.056–0.25	10	10
	Lara-Lara <i>et al.</i> , 1990	Columbia Estuary (USA)	Bimonthly	1	May	16.4	0.062–2.17	0.036–0.1	10	2
	Moll, 1977	Flax Pond (USA)	Weekly	2	March, September	4, 6	0.005–0.24		2	1.8
	Bruno <i>et al.</i> , 1983	Pedonic Bay (USA)	Biweekly	2	January, September	86.7, 80	0.12–1.59	0.2–0.54	2	0.3
	Iordan <i>et al.</i> , 1991	Rhode River Estuary (USA)	Weekly	2	May, August	10, 12	0.25–1.6		1.2	4
	Durbin <i>et al.</i> , 1975	Narragansett Bay (USA)	Biweekly	2	February, July	30				
	Cechova and Davis, 1973	San Antonio Estuary (USA)	Monthly	1	April	6, 9				
	Spies and Parsons, 1985	Fraser River Estuary (Canada)	Monthly	2	April, July					
	Radach <i>et al.</i> , 1990	German Bight (Germany)	Weekly	2	May, August					
OCE	Carpenter, 1971	Cape Fear (USA)	Monthly	1	June	15	0.018–0.23	0.0095–0.28	5	2.2
	Riley <i>et al.</i> , 1956	Long Island Sound (USA)	Weekly	1	March	60		0.0004–0.0051	20	0.3
	Herreta and Margalef, 1957	Castellon Coast (Spain)	Weekly	1	February	3.5			74.8	0.3
	Margalef and Ballester, 1967	Catalonian Coast (Spain)	Monthly	2	March, November	2.6, 13.4			63.3	0.3
	Flos, 1982	Vizcaya Coast (Spain)	Monthly	2	March, September	6.5, 4			80	0.3
	Coste <i>et al.</i> , 1977	Lyons Gulf (France)	Monthly	1	January	3			750	
	Fernández and Bode, 1991	Cantabrian Sea (Spain)	Monthly	2	April, September	2, 2	0.0005–0.01			
	De Angelis, 1956	Napoli Gulf (Italy)	Monthly	2	March, October	6	0.00006–0.055	0.000096–0.00047	90	0.3
	Ibarra, 1981	Banyuls Coast (France)	Monthly	1	January	0.8, 0.03				
	Ignatiades, 1969	Aegean Sea (Greece)	Biweekly	2	March, October					
	Bernhard <i>et al.</i> , 1969	Ligurian Coast (Italy)	Monthly	1	September					
	Grillini and Lazzara, 1978	Capo d'Uomo (Italy)	Monthly	2	February, November	0.49, 0.11			12.5	0.3
	Mura <i>et al.</i> , 1996	Bianes Coast (Spain)	Weekly	2	March, August					
	Bursa, 1961	Barent Sea (Russia)	Biweekly	2	May, August					
	Roman <i>et al.</i> , 1983	Florida Keys Coast (USA)	Monthly	1	May	0.65	0.0063–0.04		30	0.5
	Mandelli <i>et al.</i> , 1970	Long Island Coast (USA)	Monthly	2	March, October	7.5, 9	0.03–0.185	0.065–0.132	13.5	0.3
	Azov, 1986	Neritic Levant basin (Israel)	Biweekly	2	March, October	1, 0.5	0.068–0.48	0.0067–0.187	30	0.3
	Azov, 1986	Pelagic Levant basin (Israel)	Biweekly	2	March, November	0.5, 0.25	0.07–0.2	0.0038–0.024	250	0.3
	Horwood, 1982	West North Sea (UK)	Triweekly	2	April, September	2, 1	0.0062–0.37	0.014–0.058		
	Estrada, 1980	Besos Coast (Spain)	Monthly	2	March, October					
	Robinson <i>et al.</i> , 1993	Vancouver Coast (Canada)	Weekly	2	March, June	8, 21			200	
	Lakkis and Novel-Lakkis, 1980	Beirut Coast (Lebanon)	Monthly	2	May, October	1.8, 0.8			200	
	Garrison, 1979	Monterey Bay (USA)	Biweekly	1	April	22.8			150	
	Kuoppo, 1994	Gulf of Finland (Finland)	Biweekly	2	April, September	9.5, 5.6			40	
	Bustillos-Guzman <i>et al.</i> , 1995	Villefranche-Sur-Mer Coast (France)	Biweekly	2	March, October					
	Kiffe and Purdie, 1993	Southampton (UK)	Monthly	1	May	20	0.05–1.25	0.015–0.06		2.4
	Renk, 1973	Southern Baltic Sea (Poland)	Monthly	2	April, November	18, 6.5				0.5
	Estrada, 1982	Punta Endata (Spain)	Monthly	2	March, October					

Table II. Comparison of interannual variability in phytoplankton dynamics in some ECE and OCE compiled (n.a., not available)

Type of system	Reference	Location	Year	Number of biomass peaks	Months of biomass peak
ECE	Vives and López-Benito, 1957	Ria de Vigo (Spain)	1954	2	January, September
			1955	2	April, September
			1956	2	May, September
	Cadée and Hegeman, 1974b	Western Wadden Sea (The Netherlands)	1968	2	May, October
			1969	3	January, May, October
			1970	2	May, November
			1971	2	May, October
			1972	3	January, April, October
	Bollens <i>et al.</i> , 1992	Dabob Bay (USA)	1983	2	April, October
			1984	2	March, October
	Jordan <i>et al.</i> , 1991	Rhode River Estuary (USA)	1978	1	August
			1979	n.a.	n.a.
			1980	2	May, September
			1981	2	May, September
			1982	2	April, September
			1983	2	May, September
			1984	2	May, August
			1985	2	April, October
			1986	2	April, August
			1987	2	April, September
OCE	San Feliu and Muñoz, 1975	Castellon Coast (Spain)	1957	2	February, November
			1961	2	February, November
			1962	1	March
			1970	2	February, December
	Margalef and Castellví, 1967	Catalonian Coast (Spain)	1966	2	March, November
			1967	2	February, December
	Mura <i>et al.</i> , 1996	Blanes Coast (Spain)	1992	2	February, August
			1993	2	January, August

winter and spring in temperate OCE (Figure 1), although statistical differences in the timing of peak biomass between ECE and OCE could not be concluded (χ^2 , $P > 0.05$). Moreover, unimodal cycles peaked at a wider range of months in OCE ($H' = 0.82$) than in ECE ($H' = 0.75$), although these differences were not significant (t -test, $P > 0.05$).

Bimodal cycles peaked mostly in spring and late summer in ECE, whereas they peaked mostly in late winter and fall in OCE (Figure 2). In fact, bimodal cycles exhibited later first and earlier second peaks in ECE than they did in OCE (χ^2 , $P < 0.05$). Moreover, bimodal cycles peaked at a wider range of months in ECE ($H' = 0.71$ and 0.64 for the first and second peak, respectively) than they did in OCE ($H' = 0.45$ and 0.55 , respectively; t -test, $P < 0.05$ for both peaks).

Unimodal cycles commonly reached higher biomass peaks in ECE than they did in OCE (Figure 3), although significant differences in the magnitude of peak

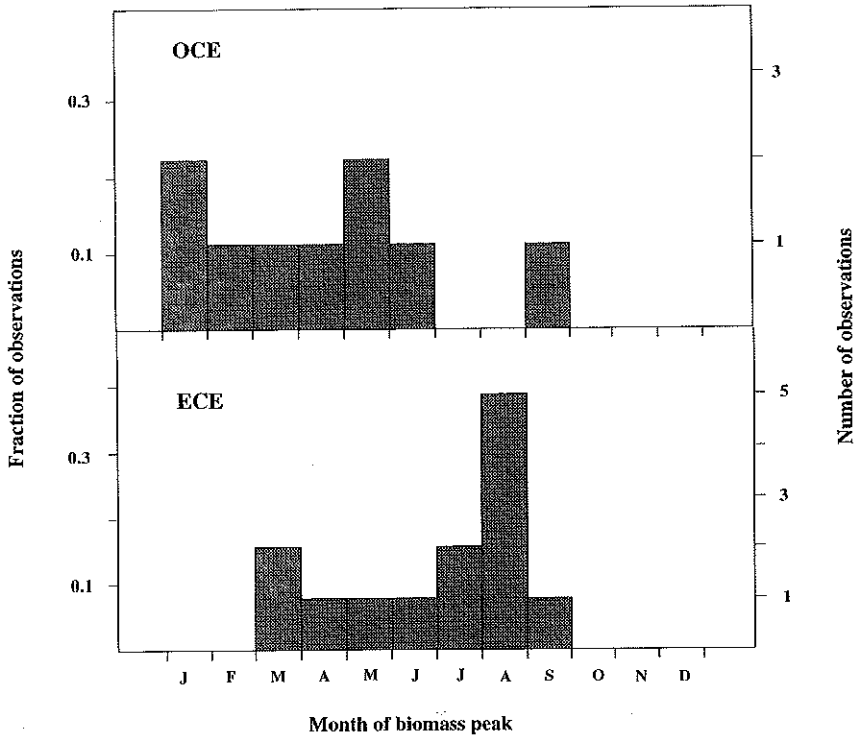


Fig. 1. Histogram of the month of peak biomass in temperate ECE and OCE with unimodal cycles.

biomass between ECE and OCE could not be concluded (Kolmogorov–Smirnov test, $P > 0.05$). Bimodal cycles, however, attained higher biomass peaks in ECE than they did in OCE (Figure 4), both for the first and second peaks (Kolmogorov–Smirnov test, $P < 0.05$).

ECE exhibited higher maximum nutrient concentrations than did OCE (Table I; ANOVA, $P \leq 0.05$). Bimodal cycles tended to show later peaks in deeper ECE (regression analyses of month of peak biomass as a quadratic function of depth: $R^2 = 0.2$, $P = 0.06$ for the first peak; $R^2 = 0.26$, $P < 0.05$ for the second peak; Figure 5a). Moreover, no unimodal cycles were found in ECE deeper than 30 m (Figure 5a), although significant differences in mean depth between ECE with unimodal cycles and ECE with bimodal cycles could not be concluded (ANOVA, $P > 0.05$). Conversely, depth did not have any effect on the timing of peak biomass and type of annual cycle (unimodal versus bimodal) in OCE (Figure 5a). The timing of peak biomass and cycle typology was also independent of tidal range in ECE and OCE (Figure 5b).

Discussion

Our results identify general seasonal trends in phytoplankton biomass in northern temperate ECE and OCE. We show that general patterns in the number and

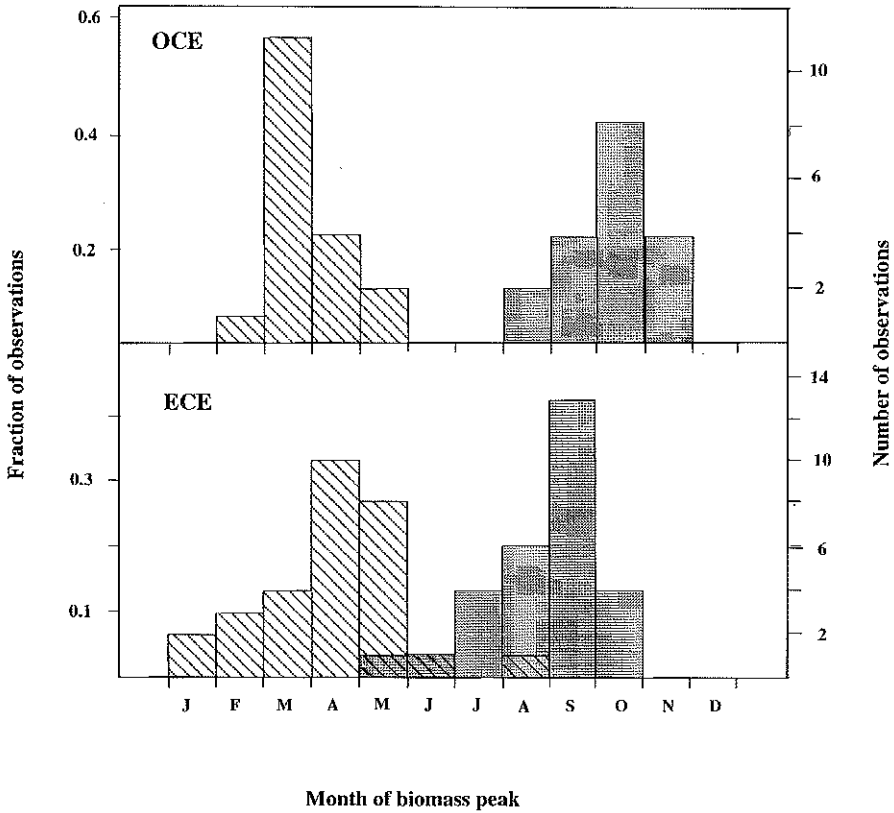


Fig. 2. Histogram of the months of peak biomass in temperate ECE and OCE with bimodal cycles. Hatched and solid bars correspond to the first and second peaks, respectively.

timing of annual biomass peaks can be discerned in these ecosystems in spite of the fact that phytoplankton dynamics often shows substantial spatial and temporal variability. Both types of ecosystem mostly display bimodal cycles with a first peak in late winter/spring and a second one in late summer/fall (Figure 2), in accordance with the classical spring-fall oscillation reported for many temperate locations (Sverdrup, 1953; Cushing, 1959; Colebrook, 1979; Harris, 1986). That suggests that phytoplankton bloom initiation due to thermocline formation in spring, subsequent collapse due to nutrient depletion and grazing pressure in summer, and bloom regeneration due to thermocline erosion and nutrient inputs in fall, are prevalent controls of phytoplankton temporal dynamics in northern temperate ECE and OCE.

However, our results reveal differences in phytoplankton seasonality between northern temperate ECE and OCE. Whereas unimodal cycles peak throughout winter and spring in temperate OCE, they mostly peak in summer in temperate ECE (Figure 1). Three mechanisms may explain these differences. Firstly, a fall

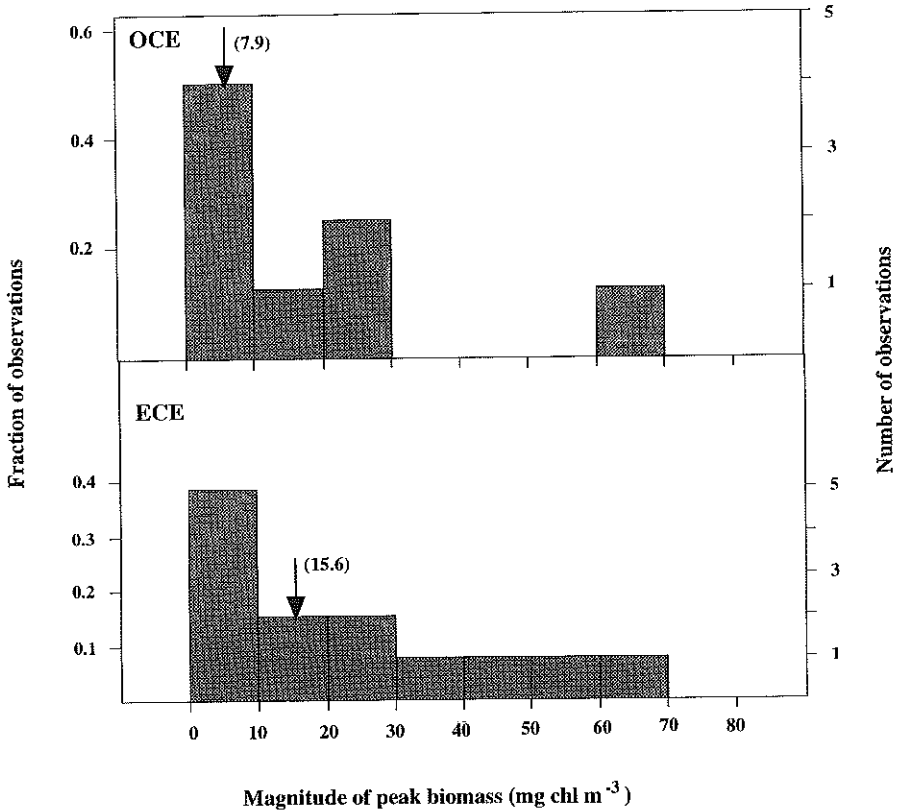
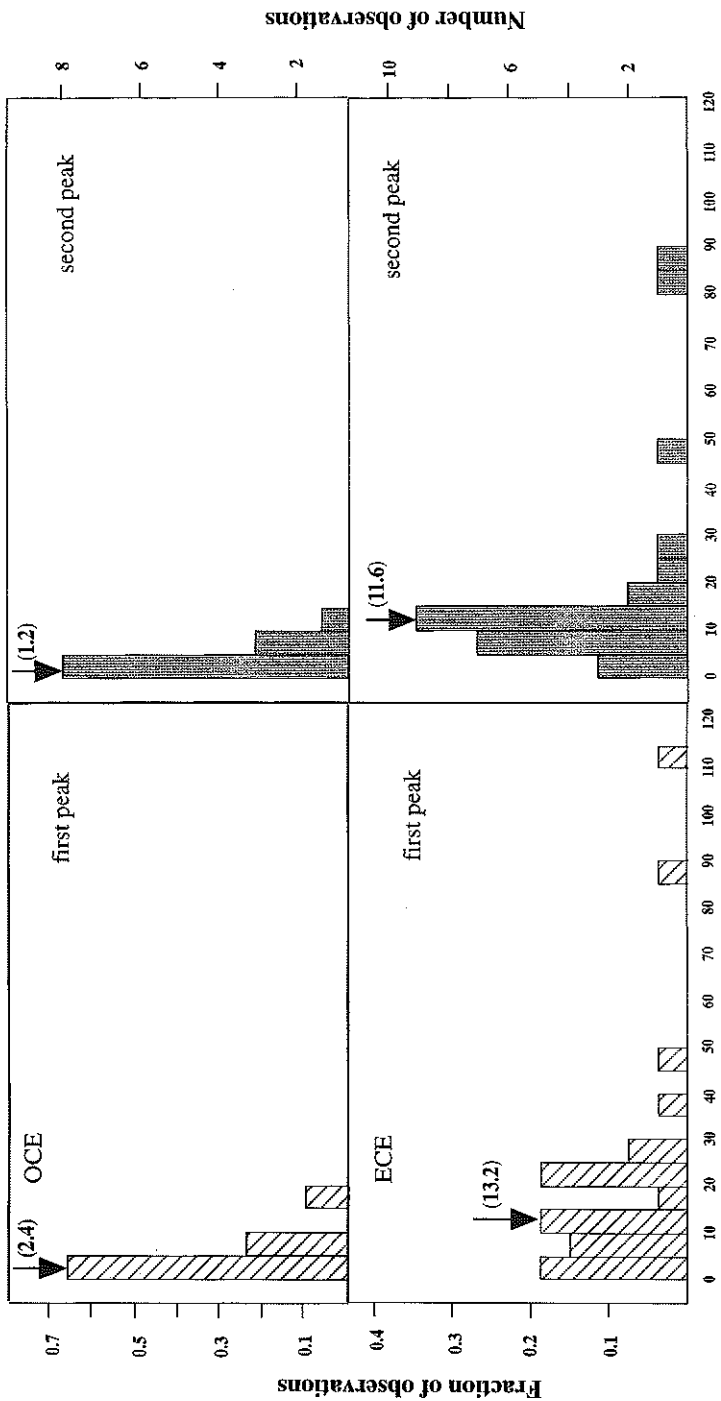


Fig. 3. Histogram of the magnitude of peak biomass in temperate ECE and OCE with unimodal cycles. Arrows indicate medians (in parentheses).

bloom does not always occur in temperate OCE, in agreement with many past reports (e.g. Colebrook, 1982; Longhurst, 1995). Hence, unimodal cycles in temperate OCE result from the suppression of the fall bloom, as shown by the fact that the annual peak of unimodal cycles and the first peak of bimodal cycles occur during the same season in temperate OCE (Figure 5a). Secondly, some temperate ECE receive high nutrient inputs persistently throughout the year from largely urbanized watersheds, which relaxes nutrient limitation of phytoplankton growth. As a consequence, water column stratification becomes the most important limiting factor of phytoplankton growth, and phytoplankton biomass annual oscillations match those in temperature and associated water stratification. If nutrient inputs are not maintained in temperate ECE throughout the summer, then phytoplankton growth prompted with the onset of spring stratification would collapse under nutrient depletion and the classical spring-fall oscillation would be displayed. This hypothesis is supported by the fact that the ECE compiled showing a summer peak tend to have higher water column nutrient concentrations than the ECE showing a bimodal cycle (Table I). In addition, past compilations also show



Magnitude of peak biomass (mg chl m⁻³)

Fig. 4. Histogram of the magnitude of peak biomass in temperate ECE and OCE with bimodal cycles. Hatched and solid bars correspond to the first and second peaks, respectively. Arrows indicate medians (in parentheses).

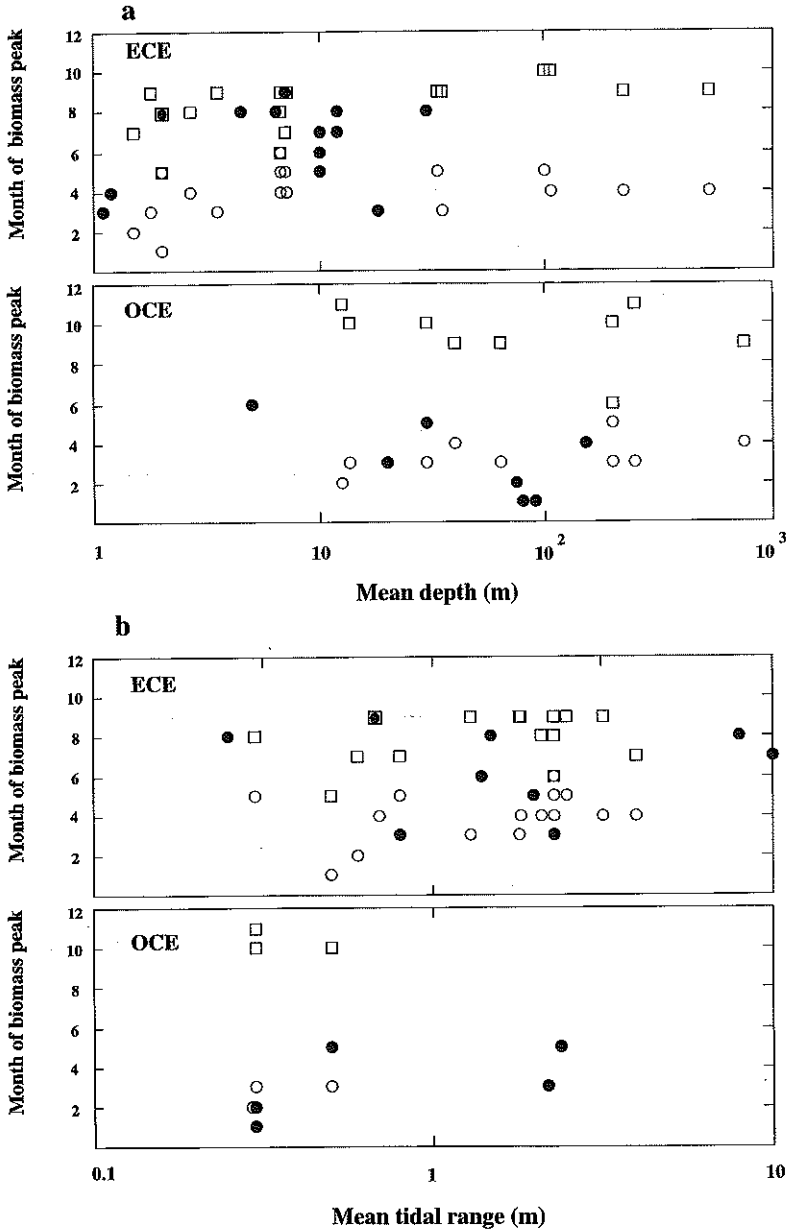


Fig. 5. (a) The relationship between month of biomass peak and mean depth in temperate ECE and OCE. (b) The relationship between month of biomass peak and mean tidal range in temperate ECE and OCE. Solid circles represent ecosystems with unimodal cycles, whereas open circles and squares represent the first and second peaks in ecosystems with bimodal cycles.

that estuaries with persistent, high nutrient loadings exhibit enhanced phytoplankton growth in summer (Valiela, 1995). Thirdly, restricted depth in ECE may also alleviate nutrient limitation of phytoplankton growth by facilitating the injection of resuspended nutrients into the mixing layer, thereby coupling phytoplankton biomass temporal oscillations with temperature seasonality (Valiela, 1995). This conjecture is supported by the fact that ECE showing a summer peak are commonly less deep than ECE with bimodal cycles (Figure 5a).

Moreover, bimodal cycles exhibit later first peaks and earlier second peaks in northern temperate ECE than they do in northern temperate OCE (Figure 2). This is counter to the conclusions arrived at by other authors (Parsons and Le Brasseur, 1968; Sinclair *et al.*, 1981). That spring blooms in temperate ECE are delayed relative to those in temperate OCE suggests that greater light intensities and water stability (i.e. later spring month) are required to counteract some negative effect on phytoplankton growth and initiate the phytoplankton bloom in temperate ECE. Such a negative effect may be the substantial turbulence levels often entailed by tidal stirring in ECE (Cloern, 1991; Monbet, 1992). This hypothesis is supported by a tendency towards lower first peaks with greater tidal ranges in ECE (Table I; $r = -0.50$, $P = 0.06$). This argument would also explain why fall blooms occur earlier in temperate ECE, since larger levels of turbulence associated with greater tidal ranges would entail a greater disruption of the summer thermocline and advance the timing of fall bloom. Yet, this hypothesis is not fully supported by our results since the timing of peak biomass is independent of tidal range in the ECE compiled (Figure 5b). Clearly, more research is needed to disclose the factors responsible for the differences in timing of bimodal cycles between temperate ECE and OCE. One of these factors could perhaps be the higher particle concentrations often encountered in ECE waters, which would demand larger light intensities (i.e. later month) for the onset of spring phytoplankton growth and would allow fall blooms to occur only with relatively high light levels (i.e. earlier month).

We also show that bimodal cycles peak at a wider range of months in temperate ECE than they do in temperate OCE. Our results suggest that these differences are due to the interaction between light seasonality and restricted depth in ECE (Figure 5a). In shallower ECE, lower light and temperature levels (i.e. earlier spring months) may be sufficient for the euphotic layer to encompass the mixed layer and trigger the spring bloom, whereas deeper ECE (i.e. greater water masses) would require greater light intensities for bloom initiation. Likewise, smaller drops in light intensity (i.e. earlier fall months) could generate sufficient thermocline erosion to initiate the fall bloom in shallower ECE, but greater drops would be required in deeper ECE (Figure 5a).

Another difference in phytoplankton dynamics between northern temperate ECE and northern temperate OCE is that bimodal cycles reach greater biomass peaks in ECE (Figure 4). That could be due to the higher nutrient concentrations found in the water columns of temperate ECE (Table I), since phytoplankton growth in coastal environments is limited by water nutrient concentrations. Accordingly, phytoplankton production is usually higher in estuaries than in open coastal locations (Smith and Hollibaugh, 1993).

In summary, our results allow consensus about the occurrence of general seasonal patterns in phytoplankton biomass in northern temperate ECE and OCE. We identify broad-scale, distinct seasonal patterns in ECE and OCE, and suggest some physical properties of ECE as causes of these differences. ECE subject to persistent, high nutrient inputs may show unimodal cycles with summer peaks because relaxation of nutrient limitation of phytoplankton growth may match biomass temporal oscillations with temperature and water stratification seasonality. Restricted depth in ECE, by facilitating nutrient resuspension into the mixed layer, may also contribute to coupling phytoplankton dynamics with temperature seasonality. Unimodal cycles in temperate OCE seem to result from abortion of fall blooms. Bimodal cycles peak at a different time and over a wider range of months in temperate ECE than they do in temperate OCE. We suggest that these differences result from the effects on phytoplankton growth of the interaction between restricted depth and light seasonality in temperate ECE. Bimodal cycles also reach higher biomass peaks in temperate ECE, which must be due to higher nutrient concentrations. Confirming these hypotheses would identify driving mechanisms of broad-scale patterns in phytoplankton dynamics.

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