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RESEARCH ARTICLE

Phytoplankton community structure and primary production in small intertidal estuarine-bay ecosystem (eastern English Channel, France)

**Fabien Jouenne · Sébastien Lefebvre ·
Benoît Véron · Yvan Lagadeuc**

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Abstract From May 2002 to October 2003, a fortnightly sampling programme was conducted in a restricted macrotidal ecosystem in the English Channel, the *Baie des Veys* (France). Three sets of data were obtained: (1) physico-chemical parameters, (2) phytoplankton community structure illustrated by species composition, biovolume and diversity, and (3) primary production and photosynthetic parameters via P versus E curves. The aim of this study was to investigate the temporal variations of primary production and photosynthetic parameters in this bay and to highlight the potential links with phytoplankton community structure. The highest level of daily depth-integrated primary production Pz (0.02–1.43 g C m^{-2} d^{-1}) and the highest maximum photosynthetic rate $P^{B}{}_{max}$ (0.39–8.48 mg C mg chl a^{-1} h^{-1}) and maximum light utilization coefficient α^{B} [0.002–0.119 mg C mg chl a^{-1} h^{-1} (μmol photons m^{-2} s^{-1})] were measured from July to September. Species succession was determined based on biomass data obtained from cell density and biovolume measurements. The bay was dominated by 11 diatoms throughout the year. However, a *Phaeocystis globosa* bloom (up to 25 mg chl *a* m^{-3}, 2.5×10^{6} cells l^{-1}) was observed each year during the spring diatom bloom, but timing and intensity varied interannually. Annual variation of primary production was due to nutrient limitation, light climate and water temperature. The seasonal pattern of microalgal succession, with regular changes in composition, biovolume and diversity, influenced the physico-chemical and biological characteristics of the environment (especially nutrient stocks in the bay) and thus primary production. Consequently, investigation of phytoplankton community structure is important for developing the understanding of ecosystem functioning, as it plays a major role in the dynamics of primary production.

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F. Jouenne (✉) · S. Lefebvre · B. Véron
Laboratoire de Biologie et Biotechnologies Marines,
UMR 100–IFREMER, Université de Caen Basse-Normandie,
Esplanade de la Paix, 14032 Caen Cedex, France
e-mail: fabien.jouenne@unicaen.fr

Y. Lagadeuc
FR/IFR CAREN, UMR-CNRS Ecobio,
Université de Rennes 1, Campus de Beaulieu,
35042 Rennes Cedex, France

Present Address:
F. Jouenne
UMR 7144–Diversity of Oceanic Plankton,
Station Biologique de Roscoff-CNRS,
Place Georges Teissier BP 74,
29682 Roscoff Cedex, France
e-mail: jouenne@sb-roscoff.fr

Introduction

Primary production is a key process in elemental cycles and trophic web dynamics (Cloern 1996), and under natural conditions photosynthetic processes related to this production of matter are constantly modified, on both short and long time-scales (Falkowski and Raven 1997). Diverse factors influencing the primary production have been studied. The majority of these studies focus on the classical relationships between photosynthesis and light availability, nutrients or temperature (Davison 1991; Lohrenz et al. 1999; Tillmann et al. 2000). Turbulence and mixing have been frequently correlated to the primary production (Levasseur et al. 1984; Demers et al. 1986; Lizon et al. 1995) and some research has compared the spatial dynamics of primary production with the distribution of chlorophyll *a* (chl *a*) (e.g. Joint and Pomroy 1993; Gaxiola-Castro et al. 1999). The influence of trophic web interactions on primary production has also been investigated (e.g. Alpine and Cloern 1992). Although the primary production has been extensively studied since Steemann Nielsen conceived the ^{14}C method in 1952, relatively few studies have included phytoplankton community structure in a multifactorial analysis of primary production dynamics (Muylaert et al. 2000; Macedo et al. 2001; Ignatiades et al. 2002).

The phytoplankton community structure can be characterized by species composition, biovolume and diversity (Côté and Platt 1983). An effort should be made to understand causes of variability in physiological and thus biological factors that play a major role in variations of depth-integrated primary production (Behrenfeld and Falkowski 1997). Microalgal population determination is essential for the understanding of primary production dynamics because it is known that the species composition influences variations of production, especially in well-mixed interface areas, such as estuaries (Malone and Neale 1981; Pennock and Sharp 1986; Shaw and Purdie 2001; Behrenfeld et al. 2004). In spite of awareness of their influence on phytoplankton dynamics, less attention has been given to the in situ impacts of biovolume (e.g. Montecino and Quiroz 2000; Snoeijs et al. 2002) and species diversity (e.g. Nuccio et al. 2003; Pemberton et al. 2004) on primary production.

The *Baie des Veys* is a macrotidal and an intertidal estuarine ecosystem (Jouenne et al 2005). Intensive shellfish farming (oysters, mussels) has been conducted in this area since the 1960s. Previous studies (e.g. Alpine and Cloern 1992) have shown that filter-feeding species (zooplankton, bivalves) have an impact on the primary production.

The aim of our study was to investigate the temporal variations of primary production and photosynthetic parameters in this bay. Besides classical environmental variables [temperature (T), salinity (S), suspended particulate matter (SPM), nutrients], particular attention was given to phytoplankton community structure [species composition, biovolume (BV), diversity (H')] in order to highlight the potential links with primary production dynamics. This study was undertaken in the *Baie des Veys* over an 18 month period from May 2002 to October 2003.

Materials and methods

Sampling area and methodology

The *Baie des Veys* is an intertidal ecosystem with a tidal range of 8 m (macrotidal) and with freshwater input mainly from the river Vire (Fig. 1). Further details on this estuarine-bay ecosystem are given in Jouenne et al. (2005).

From May 2002 to October 2003, samples were collected at five stations in the *Baie des Veys* (Fig. 1). Station N was designated as the marine station; stations E and S were, respectively, located above the northern and the southern part of the oyster park; station W was located in a non-shellfish farming zone; and station ESTUARY was situated at the mouth of the river Vire. A preliminary ACP on data from the four stations of the bay did not reveal any clusters between all samples and stations (data not shown). Since analysis of horizontal spatial variability was not the aim of this particular study, the four stations E, S, N and W are integrated here (measures averaged) into a single station renamed BAY. Vertical distribution was analysed by sampling two depths: at the surface, with the incident light intensity E_0, and at depth, with E_{20} (20% E_0). Sampling was conducted fortnightly (except in winter when monthly sampling was carried out because of the low chl *a* concentration (e.g. Reid et al. 1990; Gailhard et al. 2003), around zenith, at high tide and during spring tides (Table 1).

Chlorophyll *a* and physicochemical measurements

The Chl *a* concentration ($B^{\mathrm{chl}a}$), SPM, T, S, depth, light and nutrient [nitrate, nitrite, ammonium, silicate (Si), phosphate (P)] measurements were conducted as described in Jouenne et al. (2005). As nitrite and ammonium concentrations were negligible compared to nitrate, these three nitrogen sources are integrated in this work into a single value of dissolved inorganic nitrogen (DIN). The ratios DIN/Si and DIN/P were used to develop hypotheses on nutrient limitation.

Phytoplankton community structure

For each station and for both depths, microalgal identification (Drebes 1974; Sournia 1986; Ricard 1987; Chrétiennot-Dinet et al. 1990; Round et al. 1990; Tomas 1997), counting and measurement were carried out using light microscopy (Jouenne et al. 2005). To determine dominant species, the main criterion was the phytoplankton biomass B^{BV} [cell density (D) × BV], but qualitative microscope observations and previous

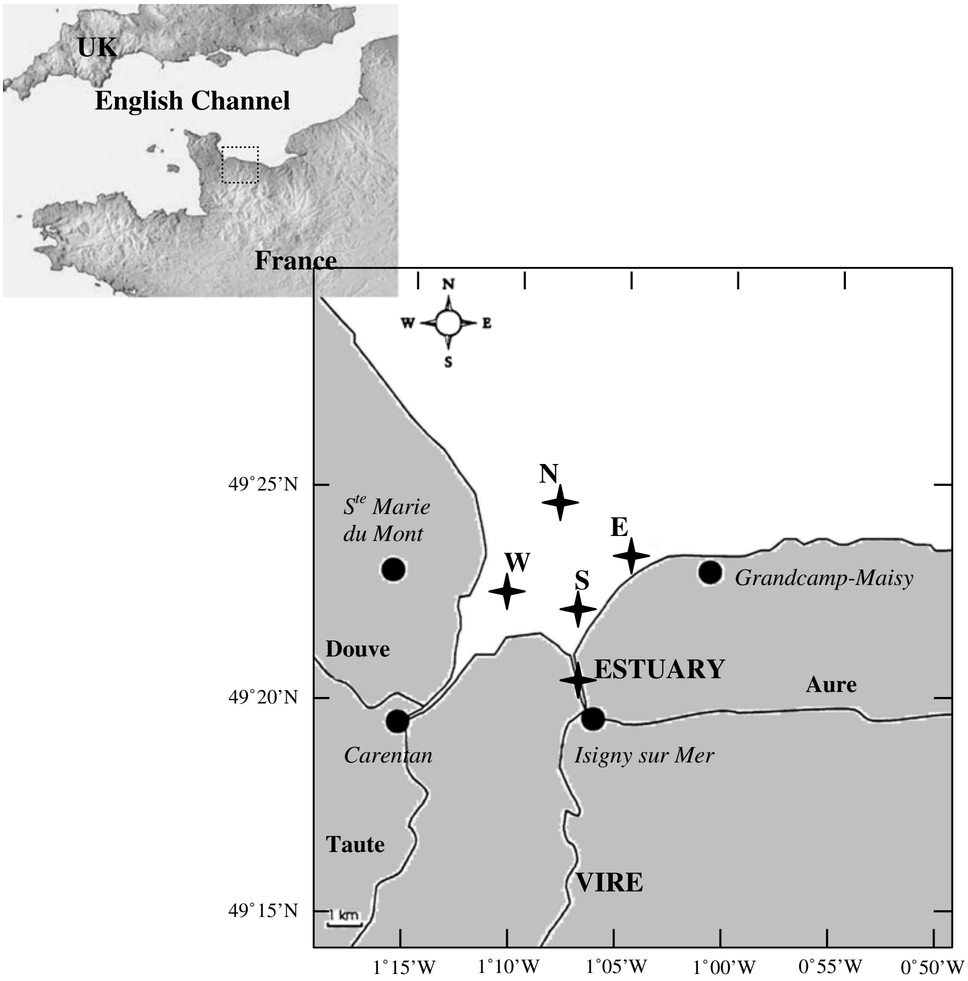


Fig. 1 The *Baie des Veys*. *Stars* show sampling stations, N (49°24′3 N, 01°06′3 W), E (49°23′5N, 1°04′7W), S (49°23′2N, 1°06′3W), W (49°23′N, 1°09′W) and ESTUARY (49°20′N, 01°05′W)

unpublished studies on the coastal waters of Normandy were also taken into account. For each dominant microalgal species, BV was measured and multiplied by D in order to obtain B^{BV} in μm^3 l^{-1} (microalgal volume per litre of seawater). At the community scale, mean BV was calculated for each sample date as the sum of all dominant species B^{BV} divided by total cell density D of these species. Size classes were arbitrarily defined based upon observations and absolute frequency analyses. The Shannon–Weaver index (H') was calculated using the whole count data, whatever be the species (Zar 1999).

Primary production

Characterizing short-term responses requires rapid and precise measurements and it is recommended to run brief simulated in situ incubations immediately after sampling (Henley 1993). Thus, the primary production measurements were conducted using the ^{14}C incorporation method (Steemann Nielsen 1952). Incubations were conducted in a radial photosynthetron (Lewis and Smith 1983; Babin et al. 1994) for 40 min (Lizon and Lagadeuc 1998). Further details are given in Jouenne et al. (2005). Results obtained were standardized to chl *a* in order to obtain estimates of primary productivity (P^B) in mg C mg chl a^{-1} h^{-1}. The model of Platt et al. (1980) was employed to fit the P versus E curves (Systat 10 software, SPSS, Chicago, IL, USA, non-linear regression model) and to estimate photosynthetic parameters: the maximum photosynthetic rate $P^B{}_{max}$, the maximum light utilization coefficient α^B, the light saturation parameter ($Ek = P^B{}_{max}/\alpha^B$) and the photoinhibition parameter (β^B) (Sakshaug et al. 1997).

The depth, light extinction coefficient (k) and photoperiod were used to calculate the daily depth-integrated primary production Pz. Measures of the light at the surface were taken every hour by DIREN and Météo-France. These measures were integrated over depth (every 0.5 m), using maximal depth and k (from in situ light measures). These results were averaged to obtain a light integrated over depth and time for 1 day.

Table 1 Sampling calendar

Date	Tidal height (m)	Rainfall (mm)	Air temperature (°C)	Wind direction	Wind speed (m s^{-1})
15th May 2002	5.9	0.6	13.2	ESE	3.2
28th May 2002	6.2	3.6	11.6	SSW	4.8
12th June 2002	5.9	1.2	14.9	WSW	5.0
26th June 2002	6.0	0.2	14.3	W	3.3
10th July 2002	5.8	0.8	14.5	SW	4.5
25th July 2002	5.9	0.6	16.7	SSW	2.5
13th August 2002	6.5	0.0	16.2	WSW	2.7
9th September 2002	6.7	33.0	13.1	S	4.3
30th September 2002	4.7	0.2	12.7	SE	2.2
24th October 2002	6.1	3.2	10.5	ND	ND
20th November 2002	6.1	3.0	8.8	ND	ND
19th December 2002	6.0	0.4	1.0	ND	ND
24th January 2003	5.9	0.2	2.4	ND	ND
20th February 2003	6.6	0.0	5.7	ND	ND
5th March 2003	6.3	2.4	10.9	ND	ND
21st March 2003	6.7	0.0	6.2	ND	ND
4th April 2003	6.1	0.0	9.1	SW	2.0
17th April 2003	6.7	0.2	11.0	ESE	2.5
6th May 2003	5.4	0.2	9.2	NW	4.2
3rd June 2003	5.6	4.8	16.3	SE	2.2
18th June 2003	5.8	0.2	16.6	WSW	5.3
16th July 2003	6.0	ND	ND	S	4.2
30th July 2003	5.9	0.8	17.0	WSW	5.2
2nd September 2003	5.9	0.0	14.8	SE	3.5
11th September 2003	6.2	0.4	17.0	W	4.2
29th September 2003	6.5	0.2	13.0	SSE	2.9
9th October 2003	6.1	0.0	14.5	ND	ND

Rainfall and wind speed are daily average values. Source: Météo-France

Wind direction: *N* north, *E* east, *S* south, *W* west. *ND* no data

Finally, the mean light in the water column Em was integrated for more than 3 days: 70% of the average light on the sample date (day 0) + 20% of the average light on day –1 + 10% of the average light on day –2 (Brush et al. 2002). The ratio Ek/Em was calculated to estimate the level of photoacclimation of the phytoplankton community. The Ek/Em ratios close to 1 illustrate a photoacclimated state (Ek and Em are almost equal); at ratios above 1, light is insufficient for optimal production (light limitation) and less than 1, light is too high to be efficiently harvested (potential photoinhibition) (Tillmann et al. 2000).

Numerical analysis

Differences between surface and depth were estimated using the non-parametric Wilcoxon test for paired samples. Principal component analyses (PCA) were performed upon data to analyse the relationships between physicochemical and biological parameters over time. The B^{BV} of dominant species was plotted in this study as an illustrative variable in order to appreciate the distribution of these species among active variables which build the axis. The PCAs were conducted using SPAD v. 4.5 software (CISIA, Montreuil, France).

Results

Temporal dynamics

Physicochemical parameters

The period of high discharge (*Q*) of the river Vire lasted from October to April, while low discharge was recorded from May to September with a minimum in August (Fig. 2a). The dynamics of sea temperature and mean light in the water column (Figs. 2b, c, 3a, b) were typical for the north-east Atlantic. The SPM was highly variable from October to April at the BAY, ranging from 4.5 to 93.4 mg l^{-1} (Fig. 3c), while at the ESTUARY (Fig. 2d) the SPM levels, ranging from 14.7 to 99 mg l^{-1}, showed greater variability throughout the year (CV = 48%). The SPM maxima were recorded during high river discharge at both stations.

At the BAY, the DIN concentration increased from August until February (from 0.1 to 37.8 μM) and then decreased rapidly from March to May (Fig. 3d). This trend was also observed at the ESTUARY (from 1.1 to 438.1 μM), but the DIN concentrations were approximately tenfold higher (Fig. 2e). The Si concentration ranged from 0.7 to

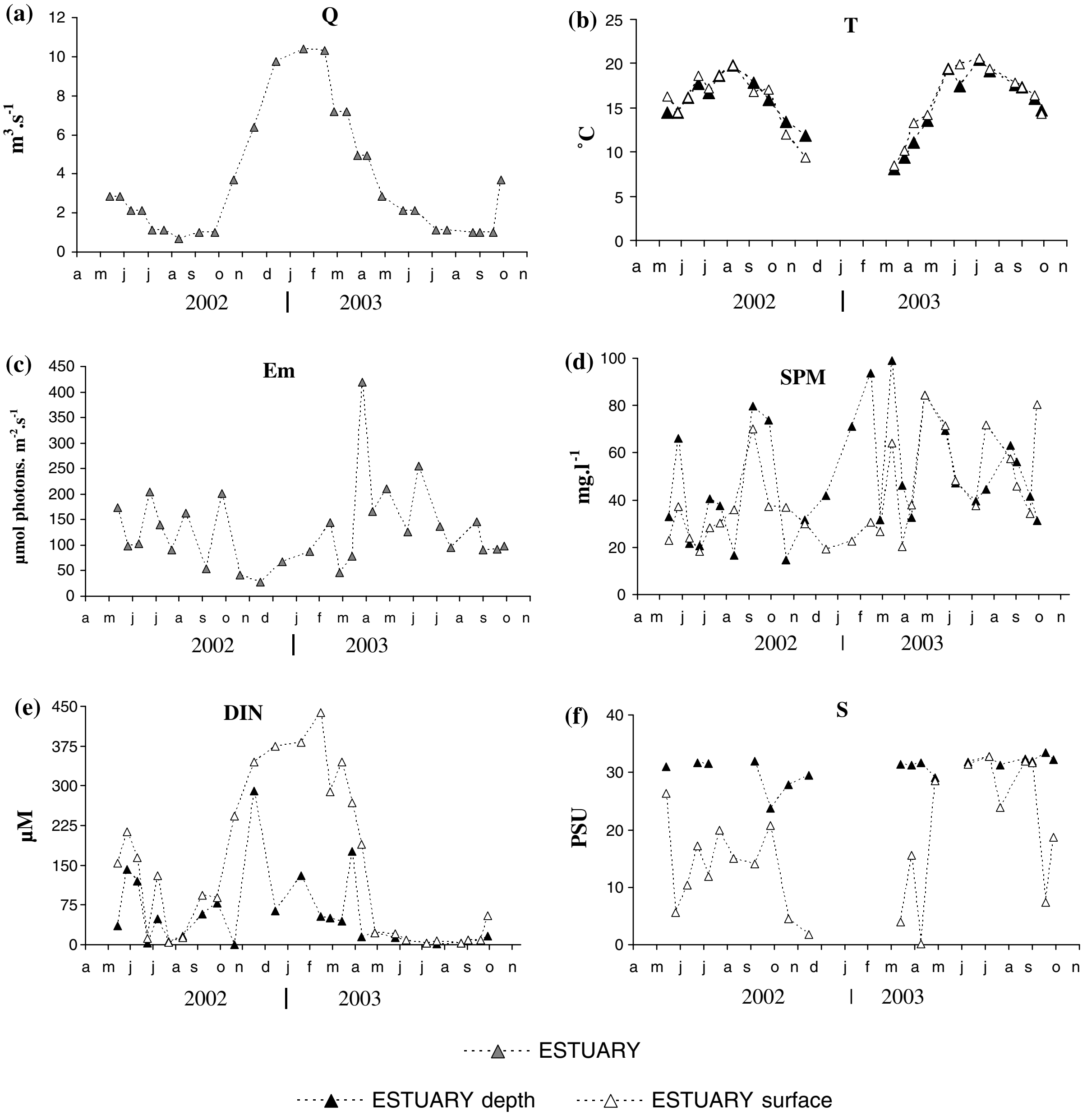


Fig. 2 Physico-chemical parameters at ESTUARY: **a** river discharge (*Q*); **b** sea temperature (*T*); **c** mean light in the water column (*Em*); **d** suspended particulate matter (*SPM*); **e** dissolved inorganic nitrogen (*DIN*); **f** salinity (*S*). *Error bars*: standard error (sometimes hidden because of its low value)

21.4 µM at the BAY, whereas at the ESTUARY it varied between 1.5 and 195 µM. The P concentration was between 0.2 and 1.5 µM at the BAY, and 0.2 and 5.1 µM at the ESTUARY. The Si and P profiles were similar to the DIN profile ($Si = 0.46DIN + 5.12$; $P = 0.007DIN + 0.76$; $P < 0.01$, $n = 265$), with a time lag leading first to the Si depletion, then to the DIN depletion. According to nutrient ratios (Fig. 4a, b), potential nitrogen limitation occurred at the BAY from late May to August in 2002 and, to a lesser extent, from June to September in 2003. At the ESTUARY, the DIN values were minimal from June to September 2003. According to the DIN/Si ratio (Fig. 4a), the Si limitation occurred from March to May 2003, at both stations. Nutrient ratios indicate that P was never limiting (Fig. 4b).

No significant difference in vertical distribution was observed for *S* (Fig. 3e), *T* (Fig. 3a), SPM (Fig. 3c) and DIN (Fig. 3d) at the BAY contrary to the ESTUARY (Figs. 2b, d–f) where each of these parameters except temperature was significantly different between surface and depth (Wilcoxon test, $P < 0.05$).

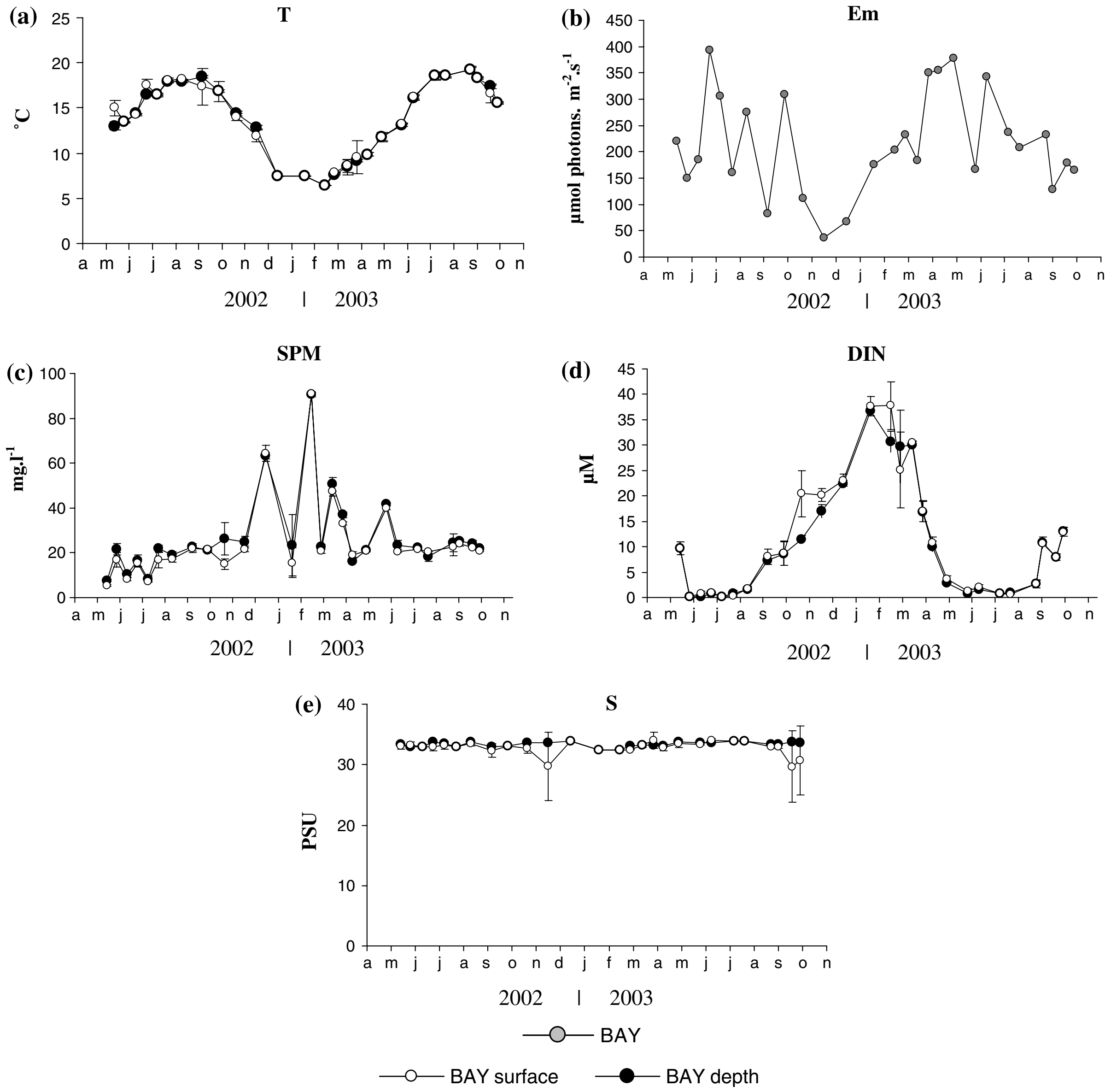


Fig. 3 Physico-chemical parameters at BAY: **a** sea temperature (*T*); **b** mean light in the water column (*Em*); **c** suspended particulate matter (*SPM*); **d** dissolved inorganic nitrogen (*DIN*); **e** salinity (*S*). *Error bars*: standard error (sometimes hidden because of its low value)

Phytoplankton community structure

Species composition One hundred and fifty-two species were observed in the *Baie des Veys* between May 2002 and October 2003 (see Appendix). Of these, 60% were *Bacillariophyceae* (i.e. diatoms), 19% were *Dinophyceae* and 12% were *Chlorophyceae s.s.*, *Euglenophyceae*, *Zygnematophyceae* and *Prasinophyceae* (hereafter referred to as green algae), the latter observed exclusively at the ESTUARY (data not shown). To complete the list, six different classes of flagellates represented 9% of all species observed. According to B^{BV} measurements, 11 diatoms were considered as the dominant species of the *Baie des Veys* (Table 2). A significant vertical difference in the distribution of B^{BV} was observed (Wilcoxon test, $P < 0.05$) only for three diatoms: *Asterionellopsis glacialis* at the BAY, *Cyclotella* sp. and *Guinardia delicatula* (syn. *Rhizosolenia delicatula)* at the ESTUARY. *A. glacialis* was primarily present at the ESTUARY, but was also identified at the BAY, mainly at the surface (concomitant with salinity decrease). *Cyclotella* sp. was observed exclusively at the surface at ESTUARY and never at the BAY. By contrast, *G. delicatula* was mainly identified

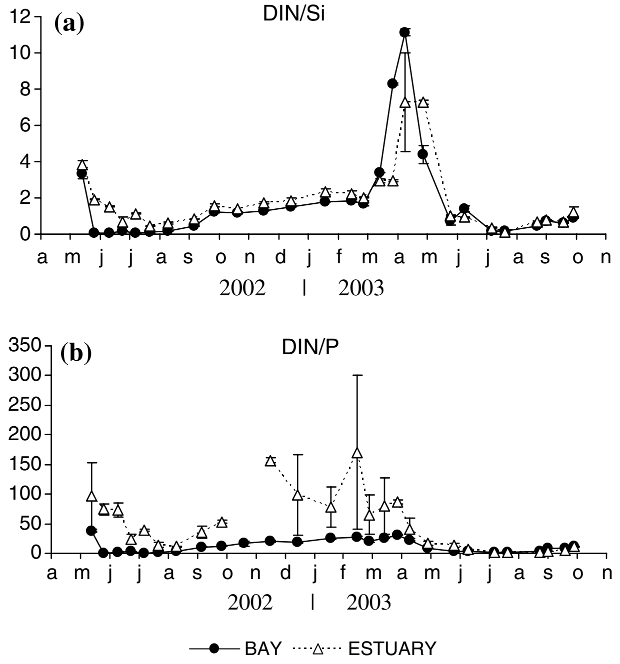


Fig. 4 Ratios DIN/Si (**a**) and DIN/P (**b**) from May 2002 to October 2003 at both stations

at the BAY and exclusively observed at depth at the ESTUARY. Vertical differences in species composition were also observed at the ESTUARY. For example, on the 24th October 2002, *Navicula* spp., *Scenedesmus quadricauda*, *Cyclotella* sp. and *Paralia marina* were observed at the surface. At depth, *A. glacialis*, *Lauderia annulata*, *G. delicatula* and *Thalassiosira* spp. were present. Taxonomic composition also differed between surface and depth at the ESTUARY on the 13th August 2002, the 30th July 2003 and the two last sample dates.

Chlorophyll a and species succession The $B^{\mathrm{chl}a}$ trends were similar at both stations, but higher concentrations were recorded at the ESTUARY (Fig. 5a, b). The $B^{\mathrm{chl}a}$ was low from late October to early March. From mid March to June, an increase was measured with a peak in April–May (25 mg m^{-3} at BAY, up to 67 mg m^{-3} at ESTUARY). The $B^{\mathrm{chl}a}$ was lower in July–August, and in September–October a second peak of lesser intensity was measured (Fig. 5a, b).

At the BAY, in late autumn and winter, *Thalassiosira rotula*, *Odontella aurita*, *Odontella regia* and *Odontella sinensis* were abundant (Fig. 6), with also *Ditylum brightwellii* and benthic diatoms, such as *P. marina* and *Fragilaria* sp., were present (data not shown). *T. rotula* (max. 74%) and *L. annulata* (max. 90%) were successively dominant in March and April. In 2003, the latter species bloomed in the whole area during March and April with $B^{\mathrm{chl}a}$ higher than 15 mg m^{-3}. The *G. delicatula* was the dominant species in May along with the prymnesiophyte *Phaeocystis globosa* (see subsequently in this section). *Guinardia flaccida* (max. 81%) and *Guinardia striata* (syn. *Rhizosolenia stolterfothii*) (max. 82%) dominated, respectively, in June and July. *Chaetoceros socialis* and *Chaetoceros debilis* were also observed in June (data not shown). In August, *O. regia* (max. 96%) was the most abundant diatom. In late summer, high levels of *A. glacialis* biomass (50%) were recorded. In early autumn, large diatoms dominated at the BAY (*Coscinodiscus wailesii* up to 96% and *O. sinensis* up to 86%) but smaller species were also identified (e.g. *Pseudo-nitzschia* sp., *C. socialis*, data not shown).

At the ESTUARY, in January and February, *O. regia* (max. 95%) and *T. rotula* (max. 59%) dominated successively (Fig. 7), with benthic diatoms also present (*P. marina*, *Navicula* spp. and *Fragilaria* sp., data not shown). These benthic species were regularly observed from autumn to early spring. Small diatoms (Table 2) were dominant in March, notably *Odontella aurita* (max. 88%). In April, *L. annulata* (max. 66%) and *G. flaccida* (max. 35%) were the most abundant species. The *A. glacialis* was present from May to October. The *G. delicatula* (max. 57%) was observed in May, then

Table 2 Dominant species: specific BV (mean ± standard error) and size structure

Dominant species	BV (μm^3 cell^{-1})	Size classes
Asterionellopsis glacialis	740 (50)	Small (<15,000 μm^3 cell^{-1})
Cyclotella sp.	1,490 (90)	
Guinardia delicatula	9,960 (920)	
Odontella aurita	11,220 (3,010)	
Lauderia annulata	29,330 (1,980)	Intermediate size
Thalassiosira rotula	32,000 (1,500)	(15,000 < BV < 15,0000 μm^3 cell^{-1})
Guinardia striata	38,200 (2,700)	
Odontella regia	186,400 (12,600)	Large (>150,000 μm^3 cell^{-1})
Guinardia flaccida	250,800 (16,000)	
Odontella sinensis	883,200 (72,800)	
Coscinodiscus wailesii	8,780,000 (1,150,000)	

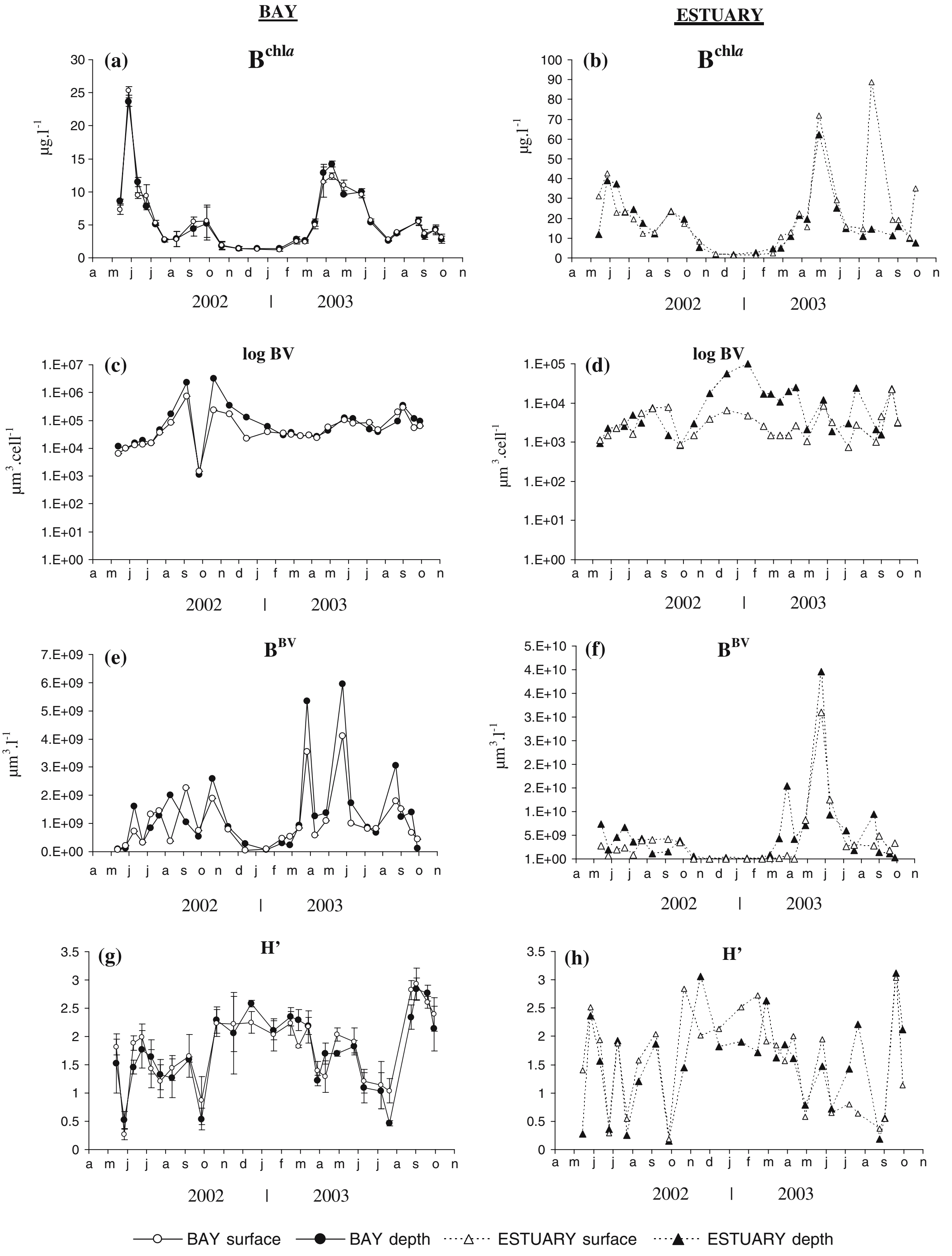
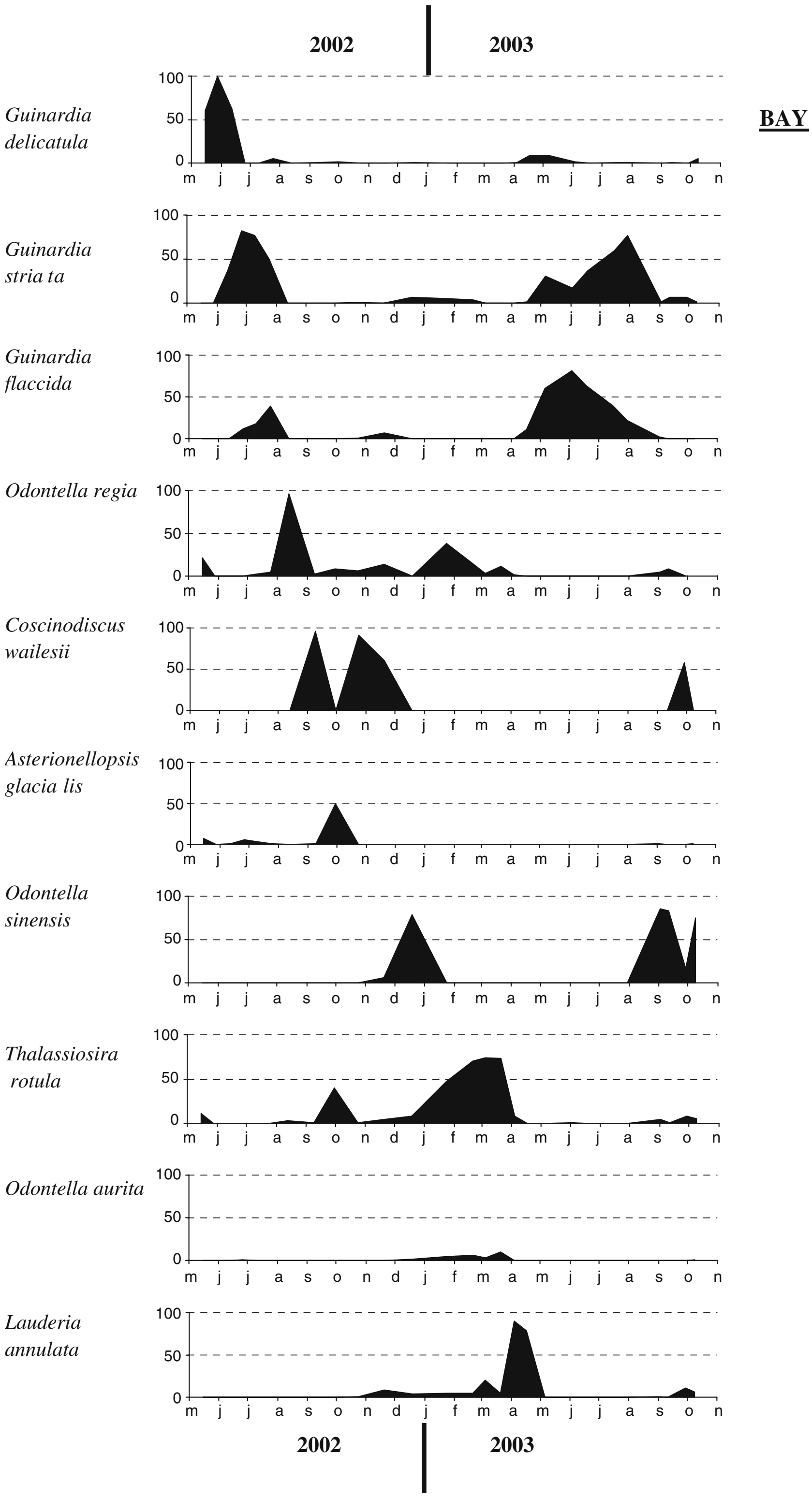


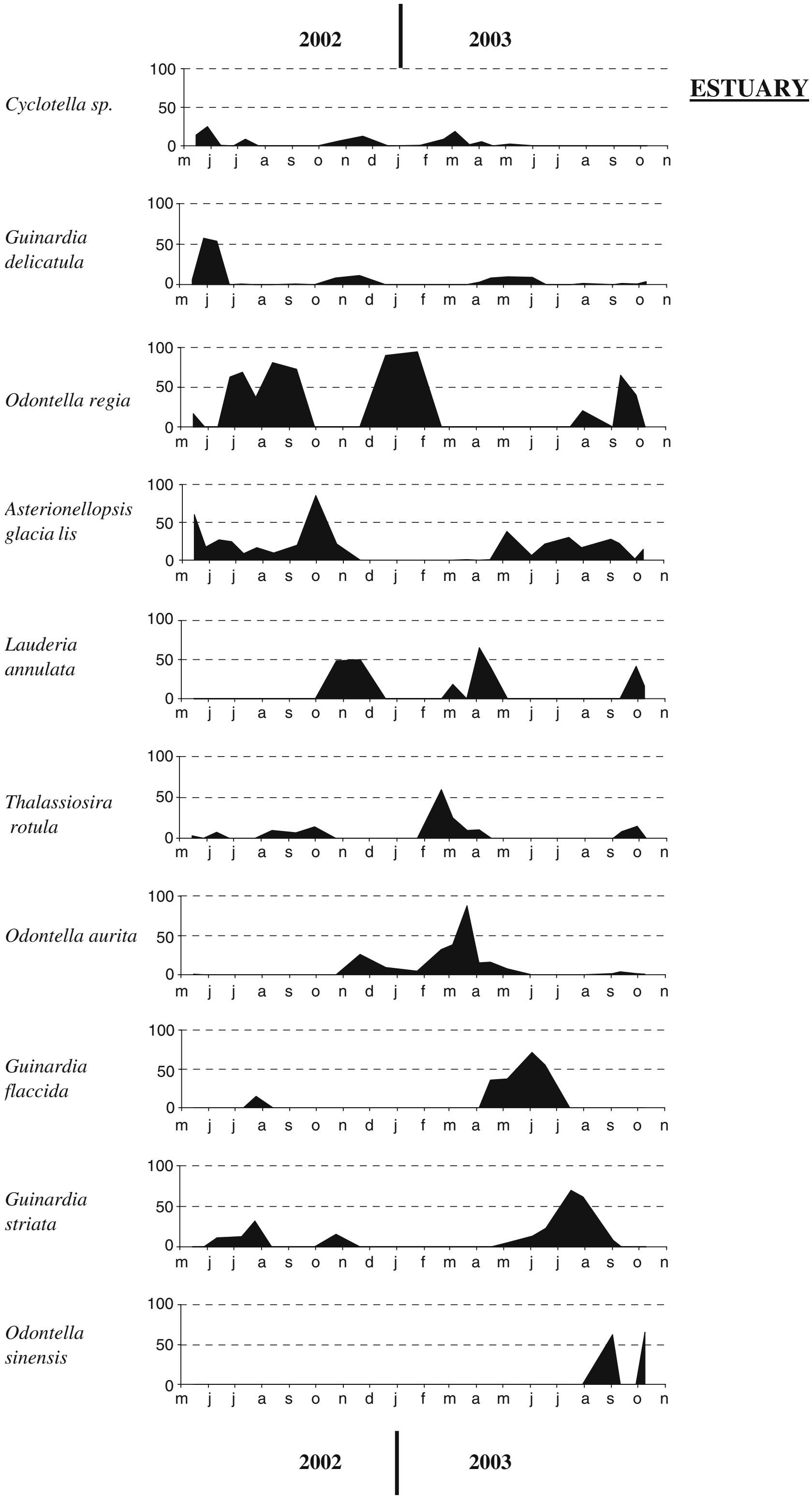
Fig. 5 Phytoplankton community structure (note the different *Y scale* between BAY and ESTUARY). **a, b** chl *a* concentration ($B^{\mathrm{chl}a}$); **c, d** mean cell biovolume (*BV*); **e, f** total phytoplankton biomass (B^{BV}); **g, h** species diversity (Shannon–Weaver index *H*′). *Error bars*: standard error

Fig. 6 Microalgal succession of dominant species at BAY from May 2002 to October 2003. Species are illustrated according to relative proportions of the total B^{BV} (%)



the *G. flaccida* (max. 71%) became the dominant species in June, and in July–August, *G. striata* (max. 70%) and *O. regia* (max. 81%) reached high contributions of the total biomass in the river. A peak in *A. glacialis* biomass was observed in late September 2002 (86%). Autumn was marked by the dominance of *O. regia* (max. 65%), *O. sinensis* (max. 65%) and *L. annulata* (max. 50%), and small benthic species

Fig. 7 Microalgal succession of dominant species at ESTUARY from May 2002 to October 2003. Species are illustrated according to relative proportions of the total B^{BV} (%)



were also observed. Throughout the sampling period, green algae were observed at the surface, especially *S. quadricauda* and *Pediastrum* sp.

In 2002, *P. globosa* bloomed throughout the studied area in late May with $B^{\mathrm{chl}a}$ higher than 25 mg m^{-3} and *D* close to 2.5 × 10^{6} cells l^{-1} (~98% of total cell density). No valid measure of biovolume could be conducted on this particular species in May 2002, and therefore it does not appear in Figs. 6 or 7. In 2003, *P. globosa* was observed in late April but its contribution to total *D* was lower (max. 5.10^5 cells l^{-1}). The increase of abundant *Phaeocystis* coincided in both years with the onset of the period of potential Si and then the DIN limitation (Fig. 4a).

Biovolume and phytoplankton biomass The BV ranged from 740 μm^3 cell^{-1} for *A. glacialis* to 8.78×10^6 μm^3 cell^{-1} for *C. wailesii* and three size fractions can be described (Table 2). Significant difference was observed at both stations between surface and depth (Wilcoxon test, $P < 0.05$; Fig. 5c, d). At the BAY, an increase in the mean community BV began in late summer in both years (Fig. 5c). The rapid decrease in late September 2002 (Fig. 5c), during neap-tide conditions, was due to an input of the small diatom *A. glacialis* at the BAY (Fig. 6). At the ESTUARY (Fig. 5d), the BV was notably higher at depth during the period of high river discharge, from October to March (Fig. 2a). The B^{BV} was higher during summer 2002 and spring 2003 at the BAY (Fig. 5e), with high levels reached in 2003. The B^{BV} was clearly higher at the ESTUARY and especially in spring 2003, when the river discharge began to decrease (Fig. 5f). At the community scale, no significant difference between surface and depth was revealed for the B^{BV}.

Species diversity The H′ was higher in autumn and winter with a sudden increase in September, in both years and at both stations (Fig. 5g, h). Values of *H′* lower than 1 occurred during three blooms at BAY: *P. globosa* in May 2002, *A. glacialis* in September 2002 and *G. striata* in July 2003 (Figs. 5g, 6). At the ESTUARY, sample dates dominated by a single species were more frequent (Fig. 5h) and they were mainly due to the *A. glacialis*, except in May 2002 with a dominance of *G. delicatula* (Fig. 7).

Primary production and photosynthetic parameters

At the BAY, the $P^B{}_{max}$ varied from 0.39 to 8.48 mg C mg chl a^{-1} h^{-1} and was higher during summer in both years (Fig. 8a). The α^B ranged from 0.002 to 0.119 mg C mg chl a^{-1} h^{-1}. (µmol photons cm^{-2} $s^{-1})^{-1}$ at the BAY (Fig. 8c) and was maximal in summer, from July to September, in both years. No significant difference between surface and depth was observed at the BAY for $P^B{}_{max}$ and α^B.

The estuarine levels of $P^B{}_{max}$ and α^B at depth mirrored the BAY values (Fig. 8a–d). At the ESTUARY, the $P^B{}_{max}$ and α^B were maximal in summer 2002 and 2003 (Fig. 8b, d). The $P^B{}_{max}$ varied between 0.35 and 7.96 mg C mg chl a^{-1} h^{-1}, and α^B was estimated between 0.001 and 0.152 mg C mg chl a^{-1} h^{-1} (µmol photons m^{-2} $s^{-1})^{-1}$. Vertical significant difference was revealed by the Wilcoxon test for the two photosynthetic parameters ($P < 0.05$).

Because most of the estimates were not significantly different from zero, photoinhibition index β^B presented few workable values.

At both stations, the primary productivity (P^B; Fig. 8e) showed the same trend than photosynthetic parameters and no significant difference was observed between surface and depth ($P < 0.05$).

The Pz (Fig. 8f) reached a minimum in December 2002 and a maximum in August 2002 at the BAY (ranging from 0.02 to 1.43 g C m^{-2} d^{-1}), while at the ESTUARY, the Pz was maximal in July 2003 and minimal in February 2003 (ranging from 0.02 to 4.06 g C m^{-2} d^{-1}). The ESTUARY levels of Pz were markedly higher than those at the BAY in summer 2003 (Fig. 8f).

At the BAY, the Ek/Em ratios (Fig. 9) were regularly under 1, while at the ESTUARY the Ek/Em was generally above 1 in 2002 and close to 1 in 2003. At both stations, the Em was often out of the optimal light harvesting range of the population observed, except in 2003 at the ESTUARY, where the Ek and Em were closer.

Primary production and phytoplankton community structure

A preliminary PCA conducted on the whole data set (27 sample dates, 5 stations, 2 depths; $n = 270$) confirmed that the four stations E, S, N and W sampled in the bay were similar and that the station ESTUARY was clearly different from the four others (data not shown). At the ESTUARY, results from sampling at high tide slack showed a two-layer system, with high nutrient concentration and low salinity at the surface (brackish water) and the opposite at depth (marine water) (Fig. 2e–f). Nutrients were assumed never to be limiting (Figs. 2e, 4a–b) and two microalgal communities were identified between surface and depth. The salinity front, which increases the inherent complexity of this station, and the sampling frequency employed in this study, masked the potential links between primary production and phytoplankton community structure.

A PCA was conducted on data from the four stations of the bay (Fig. 10a, b; 27 sample dates, 4 stations, 2 depths; $n = 216$). Component 1 accounted for 30.24% of the total variation and was negatively correlated with nutrients, SPM and H′ (Fig. 10a). Component 2 accounted for 20% of the total variation and was

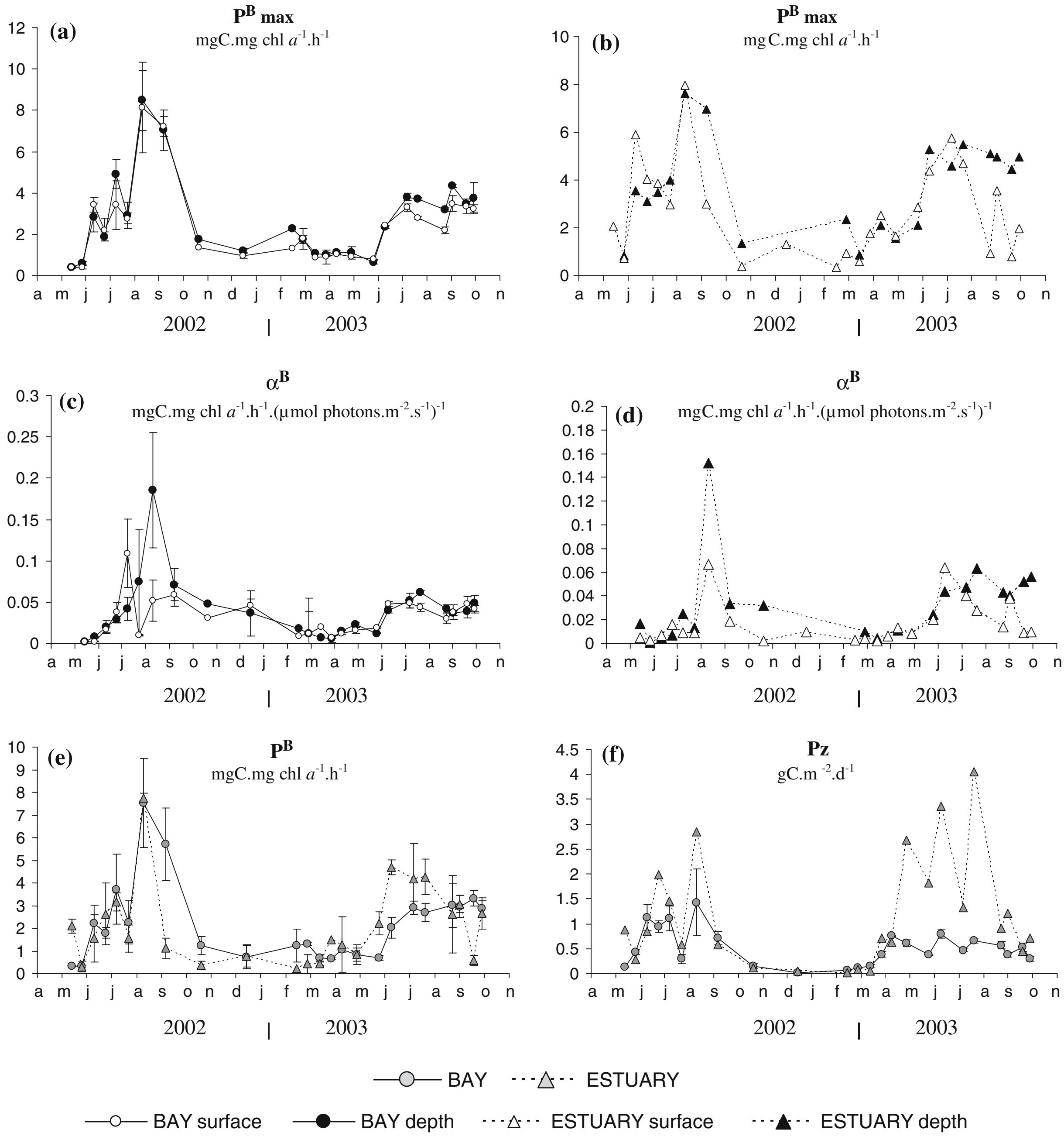


Fig. 8 Primary production and main photosynthetic parameters: **a, b** maximum photosynthetic rate P^{B}_{max}; **c, d** maximum light utilization coefficient α^{B}; **e** primary productivity P^{B}; **f** daily depth-integrated primary production *Pz*. *Error bars*: standard error

negatively correlated with P^{B}_{max}, α^{B} and T, and positively correlated with B^{chla} (Fig. 10a). Component 3 accounted for almost 10% and was positively correlated with salinity (data not shown). The two principal components allow discrimination of the samples into several clusters (Fig. 10b). The two main clusters are defined by the river discharge level Q, due to the component 1 (Fig. 10a). From autumn to early spring, Q was higher than 3 m^{3} s^{-1} (Fig. 2a) and the nutrient fluxes from the river replenished nutrient stocks in the bay (Figs. 2e, 3d). The second component superimposes three other clusters, discriminated by chl *a* concentration, primary production and photosynthetic parameters: (A) high B^{chla}, intermediate Pz and intermediate photosynthetic capacity (during spring); (B) low B^{chla}, high Pz and high photosynthetic capacity (during summer); (C) low B^{chla}, low Pz and low photosynthetic capacity (during autumn–winter)

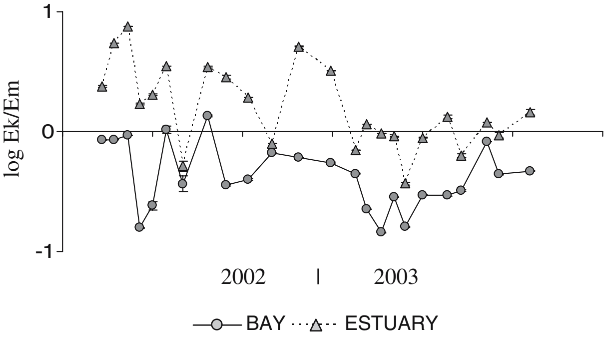


Fig. 9 Ratio Ek/Em throughout the sampling period at both stations

(Fig. 10b). Primary production Pz is positively correlated with Em and *T*, and negatively correlated to SPM and DIN (Fig. 10a).

Despite their moderate component loading, the seasonal pattern is confirmed by the species biomasses plotted as illustrative variables (Fig. 10a). Microalgal species are associated to clusters defined above, i.e. *G. delicatula* linked to cluster (A), *G. striata, G. flaccida* and *A. glacialis* linked to cluster (B) and mainly *T. rotula*, *O. aurita* and *L. annulata* linked to cluster (C). Species diversity is related to nutrient concentrations (Fig. 10a) and hence to river discharge level (Figs. 2a, 10b).

Discussion

Ecosystem dynamics and microalgal species succession

The *Baie des Veys* is a restricted macrotidal and intertidal embayment with a small catchment area compared to many other European locations (Goosen et al. 1999). Turbidity was low at the stations sampled in this study in comparison with other estuarine systems (Middelburg and Nieuwenhuize 2000), but chlorophyll *a* concentration (B^{chla}) was relatively high (Goosen et al. 1999). In winter, suspended particulate matter (SPM) concentration was generally high but variable (Figs. 2d, 3c), presumably as a result of resuspension caused by high winds in this season. The high level of river input from the Vire results in the *Baie des Veys* being rich in nutrients, and especially in the DIN, compared to other locations (Labry et al. 2002). The phosphate (P) concentration, however, was low compared to the other estuaries (Kromkamp and Peene 1995). Maximum silicate (Si) concentration at the ESTUARY was similar to that recorded in the Seine and Gironde estuaries (Aminot et al. 1998; Labry et al. 2002), whereas Si concentration was relatively low at the BAY (MacIntyre and Cullen 1996).

The period of potential nutrient limitation at the BAY was of longer duration in 2003 than in 2002 (Figs. 2e, 3d, 4a), although general levels of nutrient concentrations were similar. Precipitation levels were higher in 2002 than in 2003 (France and western Europe experienced a heat wave in the summer of 2003 (e.g. Valleron and Boumendil 2004) and thus nutrient pulses from the river are assumed to have been more regular. This difference may partially explain the elevated level of primary production in 2002 compared to 2003 at the BAY (Fig. 8f) whereas, at the ESTUARY, the primary production was higher in 2003 than in 2002, highlighting the fact that nutrients were not limiting. Potential nutrient limitation occurred earlier in 2003, before the maximal photoperiod in May–June (16 h day, 8 h night). The $B^{\mathrm{chl}a}$ during the spring bloom in 2003 was lower than in 2002 (15 vs. 25 mg m^{-3}, Fig. 5a), a fact which may be explained by the earlier onset of potential nutrient limitation in 2003. Concerning photoacclimation, the Ek/Em (light saturation parameter/mean light) ratios (Fig. 9) were close to 1 in summer 2003 at the ESTUARY, highlighting the optimal photophysiology of the microalgal community during this period.

Diatoms dominated both BAY and ESTUARY throughout the study period. In our study area the prevailing physical conditions (due to the macrotidal regime and influence of the Atlantic Ocean) are not considered favourable for growth of the smaller components of the phytoplankton as shown by Gailhard et al. (2003) in similar systems. The $B^{\mathrm{chl}a}$ levels followed a North Atlantic type seasonal cycle (Parsons et al 1984). This observation is consistent with previous studies in the English Channel and northern temperate waters (Reid et al. 1990; Cebrian and Valiela 1999; Gailhard et al. 2003). During March and April, the Si supply was exhausted mainly by the diatoms *T. rotula*, *G. delicatula* and *L. annulata*, species previously observed in this season by Escaravage and Prins (2002).

In North Atlantic temperate regions, *P. globosa* (*Haptophyta*, *Prymnesiophyceae*) generally becomes abundant following the first spring diatom bloom (e.g. Joint and Pomroy 1993; Beliaeff et al. 2001) and may dominate phytoplankton communities with a relative abundance of up to 90% of total cell density (Reid et al 1990; Lancelot and Rousseau 1994). In the *Baie des Veys* in both 2002 and 2003, *P. globosa* became competitive when the concentration of nutrients, and especially that of Si, became potentially limiting (Fig. 4a). The *Phaeocystis* cell densities may also be correlated to the DIN concentrations (Escaravage and

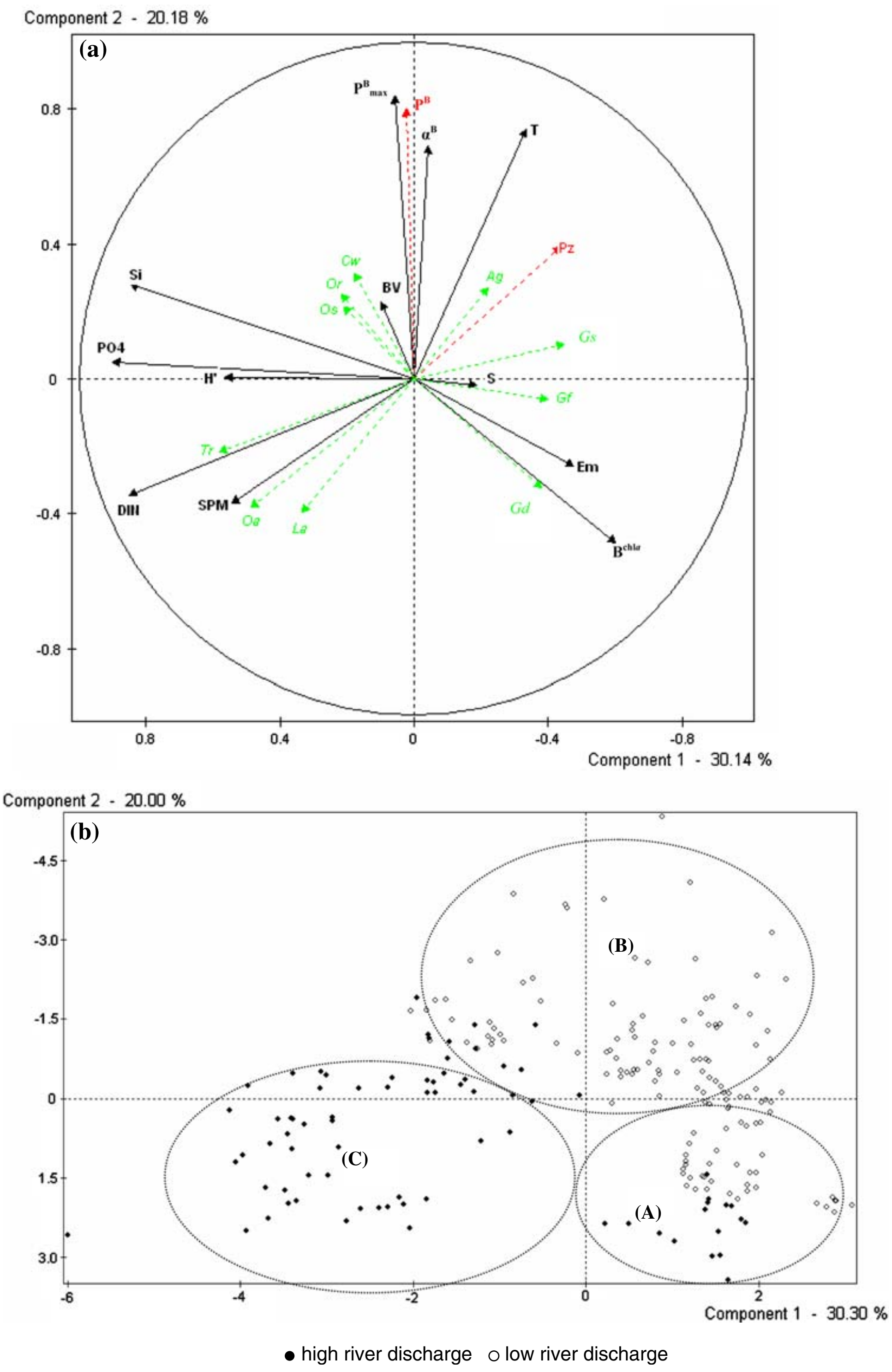


Fig. 10 **a** PCA factor loadings plot on the four stations of the bay (E, S, N and W). *Full arrows* show active variables. *Dotted arrows* show illustrative variables (variables related to primary production and species biomass). *Ag*: *Asterionellopsis glacialis*; *Cw*: *Coscinodiscus wailesii*; *Gf*: *Guinardia flaccida*; *La*: *Lauderia annulata*; *Oa*: *Odontella aurita*; *Or: Odontella regia; Os: Odontella sinensis; Gd*: *Guinardia delicatula*; Gs: *Guinardia striata*; *Tr*: *Thalassiosira rotula*. **b** PCA sample ordination plot (four stations, two depths, 27 samples) for the two first components. *A* high B^{chla}, intermediate *Pz* and photosynthetic capacity (spring); *B* low B^{chla}, high *Pz* and photosynthetic capacity (summer); *C* low B^{chla}, low *Pz* and photosynthetic capacity (autumn–winter)

Prins 2002). In our study, cell density (*D*) of *P. globosa* was fourfold lower in 2003 than in 2002. This difference might be related to the lower riverine DIN inputs in 2003. Lancelot and Rousseau (1994) stressed that the decline of *Phaeocystis* blooms is characterized by a sudden and complete disappearance of the colonies, and, in a review on phytoplankton blooms, Cloern (1996) pointed that bloom timing and duration change from one year to another. The fortnightly sampling frequency in our study may not have revealed the actual amplitude of the bloom in 2003.

In May–June, although DIN and Si were potentially limiting, two diatoms, *G. flaccida*, a large species, and *G. striata*, an intermediate size species (Table 2), dominated at the BAY (Fig. 6), as previously observed in the English Channel (Gailhard et al. 2003). In nutrient-poor environments, nutrient scarcity leads to increased microalgal nutritive resource uptake capacity (Moigis 1999). Besides, under limiting Si conditions, Escaravage and Prins (2002) observed that diatom valves were particularly thin, highlighting their capacity to reduce Si demand during limitation. The low nutrient requirements of *Rhizosolenia* might allow this species to become dominant when nutrient concentrations are sharply reduced (Raymont 1980). The poorly silicified frustule of *G. flaccida* allows it to grow during periods of Si depletion after the spring bloom (Reid et al. 1990).

In late summer and autumn, large diatoms with biovolume (BV) above 150,000 μm^3 $cell^{-1}$ were observed (*O. sinensis*, *C. wailesii*). Their presence might be due to a lower grazing pressure (e.g. zooplankton, filter feeders) in summer on these large microalgae (Dürselen and Rick 1999). Particle size distributions are closely coupled to grazing dynamics in plankton communities (Bergquist et al. 1985). Moreover, Malone (1980) stressed that many phytoplankton species possess a large vacuole within which nutrient reserves can be accumulated. The volume of this vacuole increases with the cell volume, and as this compartmentalization of elements sustains algal growth, an ability to store nutrients can favour large cells during periods of nutrient depletion.

During late autumn and winter, turbulence was enhanced and physical processes caused regulation in species composition and phytoplankton dynamics. Turbulence (macrotidal regime and high river discharge) can favour large species which are more resistant to physical disturbance, but it can also cause the resuspension of small benthic species (Alpine and Cloern 1992). Indeed, benthic and tychopelagic species (e.g. *Navicula* spp., *Fragilaria* sp., *P. marina*, *Actinoptychus senarius* (see Appendix) were identified at both stations during this period.

Primary production dynamics

Classical correlation schemes and acclimation

In comparison to other studied sites (MacIntyre and Cullen 1996; Tillmann et al. 2000), the *Baie des Veys* can be considered as an intermediately productive ecosystem. Photosynthetic parameters are consistent with values reported in previous studies (e.g. Tillmann et al. 2000; Shaw and Purdie 2001). High summer primary production values have previously been described in temperate waters [e.g. 2.2 g C m^{-2} d^{-1} in July (Tillmann et al. 2000]; >10 g C m^{-2} d^{-1} in July–August (Lohrenz et al. 1999); 1 g C m^{-2} d^{-1} in August (Joint and Pomroy 1993)). Photosynthetic parameters were maximal in summer in the Schelde Estuary (Kromkamp and Peene 1995) and in the Delaware estuary (Pennock and Sharp 1986) as in the *Baie des Veys*. High water temperature and increased light availability during the summer may explain high levels of production (Tillmann et al. 2000; Geider and MacIntyre 2002). As photosynthetic carbon assimilation is enzymatically controlled, it is a temperature-dependent process (Davison 1991; Falkowski and Raven 1997). In our study, photosynthetic parameters, Pz and *T* were positively correlated (Fig. 10a), as previously demonstrated by Lohrenz et al. (1994).

The Em was regularly different from the light saturation parameter and phytoplankton populations were seldom photoacclimated (Fig. 9). Our study area can be considered as turbulent (macrotidal regime and Atlantic Ocean influence, Gailhard et al. 2003). The frequency of destabilization in the aquatic environment determines the potential of phytoplankton production (Levasseur et al. 1984). Our observation that the likelihood of photoacclimation occurring was higher in calm conditions is coherent with previous studies (Kromkamp and Peene 1995; Lizon et al 1995; MacIntyre and Cullen 1996; Tillmann et al. 2000). Apart from the influences of Em and temperature (*T*) on primary production, although it was not a direct relationship, Pz was clearly highest when the river discharge (*Q*) was lowest (Figs. 2a, 8f). Previous authors have noted this inverse correlation between water movements and primary production (Levasseur et al. 1984; Demers et al. 1986). A previous study on the Baie des Veys was made at a shorter time-scale and similar links between mixing and primary production, especially photoacclimation, have been shown (Jouenne et al. 2005).

At both stations, high Pz and high $B^{chl\,a}$ were not always recorded simultaneously (Figs. 5a, b, 8f). The distribution of phytoplankton biomass depends, in part, on the balance between growth and mortality (Reid et al. 1990). Growth and production were high during summer despite low chl *a* and nutrient concentrations. This indicates immediate uptake of available nutrients by phytoplankton and hence no build up of nutrient stocks. Nutrient fluxes may originate from river pulses, after precipitation events, or from temperature-related increases in regeneration of nutrients in sediment matter. This latter assumption was supported by the observation that the concentration of ammonia (and not of other nutrients) increased in September (data not shown). In the *Baie des Veys*, shellfish farming is intensive (Costil et al. 2005) and filtration of phytoplankton by molluscs, notably oysters, can explain loss of biomass in summer. Moreover, a population of *Lanice conchilega* has colonized the sediment under the oyster parks, increasing the filtration process (Ropert and Dauvin 2000). The fact that Pz and B^{chla} levels were simultaneously high in summer 2003 at the ESTUARY (Figs. 5b, 8f) indicates that, besides the conditions of non-limiting nutrients, natural trophic pressure is relatively low at this location. However, no data on zooplankton dynamics or water mass turnover and export rates are available to further characterize phytoplankton biomass losses and gains within the system.

Primary production versus. phytoplankton community structure

Understanding primary production dynamics requires determination of the phytoplankton community structure. Firstly, microalgal species composition changes frequently and each species has its own photosynthetic and metabolic characteristics. Secondly, cell size variations and large ranges of biovolume can partially explain fluctuations of primary productivity. Finally, species diversity at the BAY seems to vary inversely with primary production and was influenced by nutrient resource competition.

Each season was defined by microalgal species associated to ecological characteristics. At the BAY, a seasonal cycle is illustrated by the PCA factor loading plots (Fig. 10a). Along French coasts, seasonal effects on phytoplankton dynamics have previously been illustrated by multivariate analyses (Gailhard et al. 2003). The period of highest phytoplankton production in the *Baie des Veys* (Fig. 8f, summer) was associated to the complete dominance of *G. striata* and *A. glacialis* (Figs. 6, 7, 10a). Dominance of these species has also been demonstrated over a shorter time-scale in summer 2003 (Jouenne et al. 2005). The localisation of the biomasses of these species on the PCA factor loadings plot (Fig. 10a) allows linkage of environmental characteristics to dominant 'indicator' species.

Photosynthetic parameters were also correlated to species composition (Macedo et al. 2001; Behrenfeld et al. 2004; Yoshikawa and Furuya 2004). For example, on the 24th October 2002, the maximum light utilization coefficient α^B was higher at depth (Fig. 8d) and the microalgal flora differed between surface and depth. Similar observations were made on the 13th August 2002, the 30th July 2003 and the last two sample dates. At the ESTUARY, the maximum photosynthetic rate $P^B{}_{max}$ and α^B varied between surface and depth, indicating a different physiological state of the microalgae. Some microalgae, such as *Cyclotella* sp. and *G. delicatula*, exhibited a heterogeneous vertical distribution. *Cyclotella* sp. was exclusively observed at the surface, like green algae, while *G. delicatula* was mainly present at depth at the ESTUARY.

In certain previous studies an inverse relationship between the BV and photosynthetic parameters has been found (Malone and Neale 1981; Côté and Platt 1983). According to Montecino and Quiroz (2000), variability in the relationship between cell size distribution and primary production could be explained by a differential effect of resource availability on the different size classes of phytoplankton. In our study, at the BAY, high Pz occurred concurrently with dominance of intermediate size species (Figs. 5c, 6, 8f). At the ESTUARY, in summer, when the marine influence was the highest causing influx of large diatoms from the bay, large species were identified at depth and Pz increased. Thus, in conditions of nutrient scarcity, large (*G. flaccida*) or intermediate (*G. striata*) size species are associated with relatively high Pz. Since species composition influences $P^B{}_{max}$ and α^B (see earlier) and cell size is related to Pz, this large range of biovolume can partially explain variations in photosynthetic parameters and thus Pz levels.

Recent terrestrial experiments have found that net primary productivity can often be a positive function of plant species diversity (e.g. Cameron 2002; Catovsky et al 2002; Cardinale et al 2004). However, these studies have mostly been conducted in grasslands (Hector et al. 1999) and the possibility remains that the positive diversity–production relationship does not hold in other types of ecological systems (Aoki 2003). In our case, in a marine ecosystem, species diversity (H') partially defined the cluster (C): low B^{chla}, low Pz and photosynthetic capacity (Fig. 10b). In periods of stable and high H' (Fig. 5g, h), Pz was low (Fig. 8f). In spring and summer, H' exhibited greater variability and decreased to lower levels. In a recent work in the Celtic Sea, highest primary production rates were estimated during dominance of the diatom *G. delicatula*, accounting for 72% of the phytoplankton biomass (Pemberton et al. 2004). Huston's dynamic equilibrium hypothesis which predicts maximum species richness under conditions of intermediate productivity and disturbance has been supported by the experiments of Agard et al. (1996). In this model, Huston introduced the concept of competitive exclusion, whereby species diversity is reduced under conditions of high growth, usually associated to high productivity. Species diversity can also be an indicator of bloom occurrence and thus growth increase and competitive exclusion. During bloom events, *H′* decreased (Fig. 5g, h) concomitant to high Pz (Fig. 8f). Blooms are normally dominated by one species (Reid et al. 1990). However, no clear hypothesis to define the link between diversity and primary production can be forwarded at present. A review of literature on many different ecosystems led to the conclusion that data are insufficient to resolve the relationship between diversity and productivity (Waide et al 1999).

The H′ was related to nutrients (Fig. 10a) and thus to Si concentrations. Consequently, the *H′* was probably controlled by diatom growth in the *Baie des Veys*. This relationship between the *H′* and one class of microalgae further illustrate the link between species composition (i.e. diatom dominance) and Pz, the latter being inversely related to *H′*. The effect of nutrient resources on diversity has been previously investigated (Nuccio et al. 2003; Pemberton et al. 2004). The *H′* was highest in autumn and winter, when *Q* was high and nutrients were accumulating (Fig. 10a). When trophic resources were not limiting, the *H′* was high due to a decrease in competition for nutrient resources. Nutrient inputs from the river enhanced the effect of nutrient resources on diversity at BAY. Moreover, in winter, turbulence caused by river discharge enhances inputs of freshwater species and resuspension of benthic forms, illustrating an influence of hydrodynamics on diversity (MacIntyre and Cullen 1996). The *H′* at ESTUARY was related notably to input from upstream of freshwater green algae. River runoff is a major factor influencing phytoplankton diversity and abundance (Lehman and Smith 1991).

Conclusion

In this paper, we investigated the potential link between phytoplankton community structure and photosynthetic primary production through analysis of a complex set of interactions. Annual variation of primary production was due to nutrient limitation, light climate and water temperature. Three periods have been characterized: spring with high $B^{\mathrm{chl}a}$ and intermediate Pz, summer with low $B^{\mathrm{chl}a}$ and high Pz and autumn–winter with low $B^{\mathrm{chl}a}$ and low Pz. Primary production was limited by nutrients during summer and was limited by light and temperature during autumn–winter. The paradox of having high Pz and low $B^{\mathrm{chl}a}$ during summer may be the result of trophic pressure (filter feeders). A seasonal pattern in microalgal successions was recorded. By assimilating nutrients and thus decreasing nutrient stocks, a microalgal species modifies the trophic environment and favours other species with different physiological characteristics (negative feedback). Consequently, species succession influences primary production. This seasonal pattern was recorded both years. Seasonal changes in phytoplankton biovolume can also explain Pz dynamics (link between BV and nutrient assimilation or predation). Species diversity was also related to the primary production since it was influenced by nutrient resource competition and thus river discharge. A greater understanding of the phytoplankton community structure in studying the primary production dynamics seems to be crucial.

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Appendix

List of phytoplankton taxa (Table 3)

Table 3

***Bacillariophyceae* (91)**
Benthic (23)
Craticula cuspidata
Didymosphenia sp.
Diploneis sp.
Entomoneis alata
Ephemera planamembranacea
Fragilaria sp.
Licmophora sp. (epiphytic)
Lyrella sp.
Melosira moniliformis
Navicula spp.
Navicula transitrans f. delicatula
Nitzschia longissima
Nitzschia sp.
Pinnularia sp.
Plagiotropis lepidoptera
Podosira stelliger

Table 3 continued

Bacillariophyceae **(91)**
Raphoneis amphiceros
Rhabdonema sp.
Striatella unipunctata
Synedra sp.
Benthic (tychopelagic) (5)
Actinoptychus senarius
Bacillaria paxillifera
Gyrosigma sp.
Paralia marina
Pleurosigma sp.
Pelagic (63)
Asterionella formosa
Asterionellopsis glacialis
Attheya armata
Bellerochea malleus
Cerataulina pelagica
Cerataulus turgidus
Chaetoceros constrictus
Chaetoceros costatus
Chaetoceros curvisetus
Chaetoceros danicus
Chaetoceros debilis
Chaetoceros decipiens
Chaetoceros densus
Chaetoceros diadema
Chaetoceros didymus
Chaetoceros socialis
Chaetoceros teres
Chaetoceros tortissimus
Chaetoceros sp.
Thalassiosira eccentrica (syn. Coscinodiscus eccentricus)
Coscinodiscus granii
Coscinodiscus pavillardii
Coscinodiscus radiatus
Coscinodiscus wailesii
Coscinodiscus sp.
Cyclotella sp.
Cylindrotheca closterium
Detonula pumila
Ditylum brightwellii
Eucampia sp.
Eucampia zoodiacus
Grammatophora serpentina
Guinardia flaccida
Helicotheca tamesis
Lauderia annulata
Leptocylindrus danicus
Leptocylindrus minimus
Lithodesmium undulatum
Meuniera membranacea
Odontella aurita
Odontella mobiliensis
Odontella regia
Odontella sinensis
Porosira glacialis
Pseudo-nitzschia delicatissima
Pseudo-nitzschia fraudulenta
Pseudo-nitzschia pungens
Pseudo-nitzschia sp.
Guinardia delicatula (syn. Rhizosolenia delicatula)
Dactyliosolen fragilissimus (syn. Rhizosolenia fragilissima)
Rhizosolenia imbricata
Rhizosolenia pungens
Rhizosolenia setigera
Guinardia striata (syn. Rhizosolenia stolterfothii)
Skeletonema costatum
Stephanodiscus sp.
Tabellaria sp.
Thalassiosira anguste-lineata
Thalassiosira fallax
Thalassiosira levanderi
Thalassiosira nordenskioldii
Thalassiosira punctigera
Thalassiosira rotula
Thalassiosira sp.
Thalassionema nitzschioïdes
Triceratium alternans
Dinophyceae **(29)**
Akashiwo sanguinea
Dinophysis acuminata
Diplopeltopsis minor
Gonyaulax sp.
Gymnodinium chlorophorum
Gymnodinium sp.
Gyrodinium crassum
Gyrodinium opimum
Gyrodinium spirale
Gyrodinium sp.
Heterocapsa triquetra
Katodinium glaucum
Katodinium rotundatum
Noctiluca scintillans
Oxyrrhis marina
Peridinium quinquecorne
Polykrikos schwartzii
Prorocentrum micans
Prorocentrum sp.
Protoperidinium bipes
Protoperidinium brevipes
Protoperidinium claudicans
Protoperidinium conicum
Protoperidinium minutum
Protoperidinium ovatum
Protoperidinium pellucidum
Protoperidinium punctulatum
Protoperidinium sp.
Scrippsiella trochoidea
Chlorophyceae **s.s. (12)**
Ankistrodesmus falcatus
Chlamydomonas sp.
Crucigenia sp.
Kirchneriella lunaris
Kirchneriella obesa
Micractinium sp.
Monoraphidium sp.
Pediastrum sp.
Scenedesmus acutus
Scenedesmus armatus
Scenedesmus quadricauda
Scenedesmus sp.
Chrysophyceae **s.l. (3)**
Mallomonas sp.

Table 3 continued

***Bacillariophyceae* (91)**
Ochromonas sp.
Synura sp.
***Prymnesiophyceae* (3)**
Chrysochromulina sp.
Emiliania huxleyi
Phaeocystis globosa
***Cryptophyceae* (3)**
Hemiselmis sp.
Plagioselmis sp.
Rhodomonas sp.
***Prasinophyceae* (2)**
Pyramimonas longicauda
Tetraselmis sp.
***Euglenophyceae* (2)**
Euglena spp.
Phacus sp.
***Raphidophyceae* (2)**
Fibrocapsa sp.
Heterosigma sp.
***Zygnematophyceae* (2)**
Closterium sp.
Staurastrum sp.
***Dictyochophyceae* (2)**
Dictyocha speculum
Pseudopedinella sp.
***Pavlovophyceae* (1)**
*Pavlova nov.*sp.

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