Estuarine, Coastal and Shelf Science 80 (2008) 212–224

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Short-term variability of the phytoplankton community in coastal ecosystem in response to physical and chemical conditions' changes

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ARTICLE INFO

Article history:
Received 3 April 2008
Accepted 4 August 2008
Available online 20 August 2008

Keywords:
time scale
size-fractionated biomass
macro-tidal
English Channel

ABSTRACT

The short-term dynamics (time scale of a few days) of phytoplankton communities in coastal ecosystems, particularly those of toxic species, are often neglected. Such phenomena can be important, especially since these very species can endanger the sustainability of shellfish farming. In this study, we investigated the short-term changes in phytoplankton community structure (species succession) in two coastal zones in parallel with physical and chemical conditions. Mixing events with allochtonous waters could thus be distinguished from local processes associated with population growth when it was associated with a change in light or nutrient limitation. Mixing events and water advection influenced fluctuations in total phytoplankton biomass and concentration of dominant species, while local processes influenced delayed changes in community structure. The estuarine species *Asterionellopsis glacialis* increased in concentration when the water mass mixed with the nearest estuarine water masses. The biological response, measured as photosynthetic capacity, occurred after a time-lag of a few hours, while the changes in community structure occurred after a time-lag of a few days. Finally, the coastal water mass was constantly mixed with both the nearest estuarine and marine water masses, leading in turn to delayed changes in phytoplankton community structure. These changes in species composition and dominance were observed on a time scale of a few days, which means that some toxic species may be missed with a bi-weekly sampling strategy.

1. Introduction

Temperate coastal zones represent boundaries between oceanic and continental zones, and, as biologically productive areas, are often economically important for shellfish and fish farming. Shellfish, as sedentary species, depend upon localized resources. One of their main food sources is suspended phytoplankton cells (Marin Leal et al., 2008), which live in coastal water masses whose movements rely on the tide. The phytoplankton populations, which are present in each tidal cycle at the same place, are influenced both by local (*in situ*) factors within the water mass and by horizontal transports (Cloern, 1996). Local factors, which include growth and loss factors, cause population change within a water mass (Cloern, 1996). Horizontal transports, which are driven by tidal currents, advection of water due to gradient of water density and wind stresses, cause population change when they mix populations from different waters masses (Cloern, 1996).

Strong physical and chemical forcing, such as mixing with nutrient-rich freshwater from an estuary, characterizes coastal ecosystems. Consequently, physical and chemical conditions fluctuate over different time scales, from that of the tidal cycle (two periods: 12 h and 14 days) to full seasons. Previous work has shown short-term variability of both species composition and photosynthetic capacity during tidal movement on a time scale of a few hours (Jouenne et al., 2007). Changes in photosynthetic parameters have also been associated with changes in community structure and/or with photo-acclimation processes during vertical mixing and the tide (Lizon and Lagadeuc, 1998a,b; Lizon et al., 1998). In addition, many studies have highlighted, the seasonal variability of community structure and photosynthetic parameters in coastal and estuarine zones on a bi-weekly scale (Amo et al., 1997; Jouenne et al., 2007; Lopes et al., 2007). Characteristics of annual phytoplankton community dynamics, such as photosynthetic capacity, population biomass, and dominant species are largely controlled by abiotic parameters: light and nutrient availability, mixing regime and temperature (Margalef et al., 1979; Gentilhomme and Lizon, 1998; Smayda and Reynolds, 2001). Finally, even if it is difficult to attribute recent changes in seasonal succession in coastal zones to either global warming or nutrient enrichment (Breton et al., 2006), there is little question that climate and nutrient load are both

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doi:10.1016/j.ecss.2008.08.008

considered preponderant drivers of biological activity and species composition. Physical and chemical parameters can be used to predict the occurrence of the main groups of phytoplankton. For instance, the spring decrease of siliceous algae is induced by the silicon depletion (Egge and Aksnes, 1992), while the non-siliceous species, such as *Phaeocystis* sp., decrease in density with the depletion of nitrogen (Rousseau et al., 2000). Climate can also modulate the development of algal blooms, when low horizontal transports increase hydraulic residence time within estuaries for instance (Vieira and Chant, 1993). However, it is not possible to predict which species will dominate or whether toxic species will occur. The dynamics of coastal phytoplankton species is still poorly understood, and finding the link between changes in physical and chemical parameters and their influence on the growth and competition among species represents a critical step in better understanding coastal systems.

Although these physical and chemical parameters both fluctuate at intermediate time scales (between tidal and seasonal), less is known about environmental drivers at smaller time scales. Particularly interesting is how these drivers may induce a temporary increase in population abundance over a few days, particularly in toxic species. Phytoplankton dynamics in laboratory experiments, or in mesocosms, are mainly studied on short-time scales (Fouillaron et al., 2007), while *in situ* dynamics of community structure are generally studied using a bi-weekly or monthly sampling (Jouenne et al., 2007; Spatharis et al., 2007). Less is known about the consequences of change in physical and chemical conditions for the phytoplankton community over a few tidal cycles. As a result, mixing processes between estuarine and marine waters influence water temperature, nutrient concentration and salinity. In parallel with, or perhaps resulting from, these environmental changes, biological parameters should also change. Mixing processes between estuarine and marine waters influence species composition directly through the introduction of new species and indirectly through increases in nutrient availability. Nutrient concentrations may thus be changed on a time scale of a few days and could induce transient consequences for growth, fluctuations in biomass, and competition between species. In support of this claim, a model based on a chemostat experiment demonstrated that pulsing nutrient supply can dramatically change phytoplankton community composition (Roelke et al., 1999). In addition, wind can influence mixing regimes within the water column, leading to changes in competition between fast and slow sinking species. Through mesocosm bioassays in an estuary, Pinckney et al. (1999) demonstrated that cryptomonad biomass increased under calm conditions and that chlorophyte, diatom, cyanobacterial biomass increased in mixed conditions. Lastly, since light availability can change on a time scale of a few days (e.g. input of suspended matter), such changes may also affect phytoplankton community structure, particularly in turbid nutrient-rich systems (Alpine and Cloern, 1988). All of this evidence suggests that we should also observe short-term variability in phytoplankton community structure, biomass and photosynthetic capacity in response to changes in physical and chemical conditions in coastal water masses. Coastal phytoplankton communities are regularly associated with toxin production. As a result, toxins are often stored in shellfish tissues when they filter-feed toxic species present in the farming area.

Understanding and characterizing this short-term variability in phytoplankton community structure, particularly species succession, in key areas such as aquacultural zones is important. These changes in community structure may indeed have dramatic effects on farming productions, particularly if these populations are toxic. In addition, the list of toxic species responsible for shellfish poisoning is quite long and is not specific to one class. Among the dinoflagellates, *Gymnodinium catenatum* (Estrada et al., 2007), *Pyrodinium bahamense* (Montojo et al., 2006), *Alexandrium fundyense* (Sephton et al., 2007), *Prorocentrum minimum* (Wikfors, 2005), *etc.* are identified as harmful species. Toxic species along the French coast also belong to Raphidophyceae, which include *Fibrocapsa japonica*, to Prymnesiophyceae with *Phaeocystis globosa* and *Chrysochromulina* sp., and to Diatomophyceae with *Pseudo-nitzschia* sp. (Raffin and Belin, 1998). The sustainability of shellfish farming is thus regularly threatened by the occurrence of harmful algae blooms (HABs), a growing problem for coastal regions on a global scale (Maso and Garces, 2006). In France in 2000, marine farming was closed for several weeks due to the presence of the toxin of *Pseudo-nitzschia pseudodelicatissima* and *multiseries* in shellfish (Amzil et al., 2001) and in 2004 king scallop harvesting sites in eastern English Channel were closed for several months due to contamination up to 20 μg domoic acid g^{-1} tissue and to slow toxin depuration of the scallops (Nezan et al., 2006). Resulting consequences for human health can be serious, as shown in autumn 1987 in Canada, where the accumulation of toxins produced by *P-n. delicatissima* in mussels resulted in the death of three people and the illness of 100 more (Martin et al., 1990). Based on this evidence, it is clear that understanding the short-term dynamics of coastal phytoplankton species, with a focus on toxic species, is a key issue for the risk assessment of toxicity events in shellfish tissues.

In this study, we characterized the short-term phytoplankton dynamics in response to daily changes in the physical and chemical environments in the eastern (Baie des Veys) and western (Lingreville-sur-mer) English Channel during spring and autumn. Changes in biological activity, size-fractionated biomass, and species composition were compared with the changes in temperature, salinity, nutrient and light availability using multi-variate analysis.

2. Materials and methods

2.1. Study sites

Two sampling sites were chosen in the English Channel, both located northwest of France (Normandy): Baie des Veys (eastern English Channel) and Lingreville-sur-mer (western English Channel) (see Fig. 1). Both areas sustain shellfish farming. These sites are macro-tidal ecosystems, with a maximum tidal range of 8 m, and a mean depth of 6 m. Baie des Veys and Lingreville-sur-mer represent two contrasting coastal zones, in terms of their nutrient availability and mixing opportunities with other water masses. Lingreville-sur-mer is directly exposed to westerly winds, but is not directly influenced by river discharges. Baie des Veys is influenced by higher river discharge, but is doubly protected from westerly wind because of its morphometry and its location in the eastern English Channel. The water mass of Baie des Veys's should mainly mix with freshwater water, while the water mass of Lingreville-sur-mer should be more influenced by offshore water masses. More details on these coastal areas can be found in Marin Leal et al. (2008).

Sampling was always performed at high tide at the same location (48°56′129N–1°35′656W for Lingreville-sur-mer and 49°24′50N–1°06′50 for Baie des Veys). As a result, time of sampling changed during the sampling period from early morning to middle afternoon depending on the time of high tide. Lingreville-sur-mer was sampled in spring and autumn (11/04/2006–28/04/2006 and 2/10/2006–20/10/2006), while Baie des Veys was studied only in autumn (11/9/2006–25/9/2006), due to inclement spring weather conditions.

Both sampling sites have been included in the REPHY (IFREMER) network and to the SMEL HYDRONOR data collection, which collect samples over the year and supply an environmental databank of hydrological parameters and phytoplankton communities (IFREMER/Quadrige & RHLN and Réseau SMEL HYDRONOR). Baie

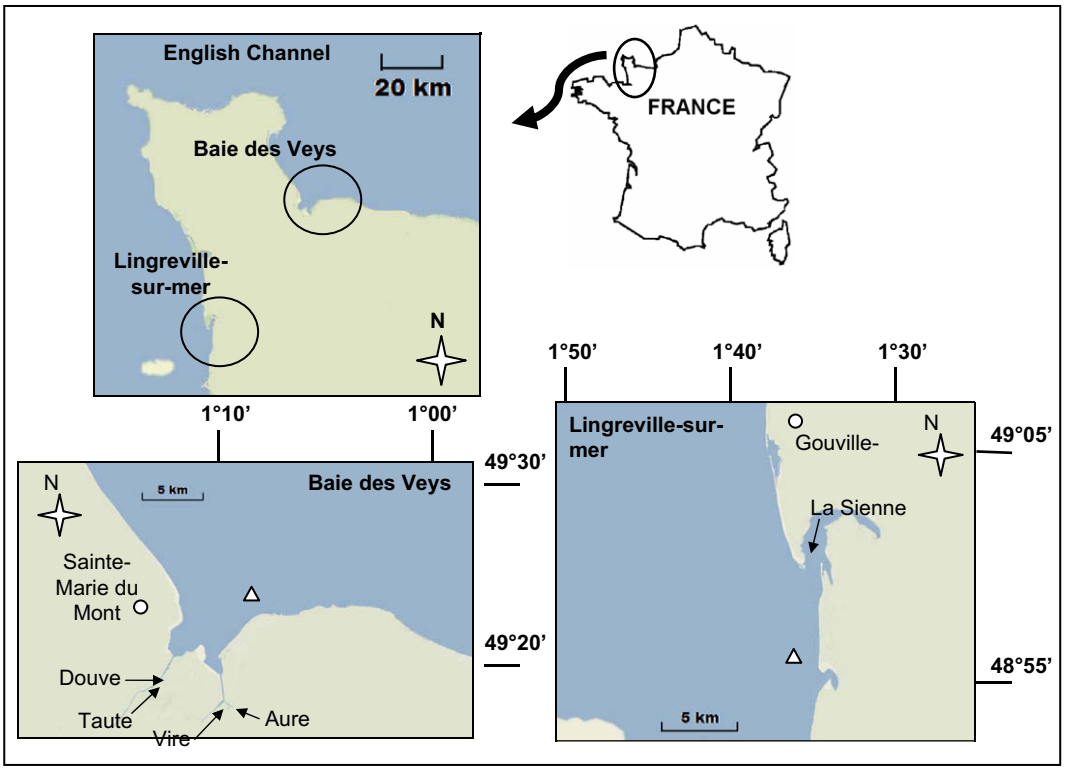

Fig. 1. Location of the sampled sites, Baie des Veys (BDV) and Lingreville-sur-mer (LGV).

des Veys was thus sampled 29 days in 2006 by the REPHY (IFREMER) network and Lingreville-sur-mer was sampled 17 days in 2006 by the SMEL HYDRONOR network. During this short-term study, Baie des Veys was sampled seven times in autumn, while Lingreville-sur-mer was sampled 18 times in spring and in autumn.

2.2. Physico-chemical measurements

Meteorological conditions were monitored by Meteo France approximately 15 km from the sampling sites (Gouville-sur-mer for Lingreville-sur-mer and Sainte-Marie du Mont for Baie des Veys), as shown on Fig. 1. Solar radiation data were collected hourly, while air temperature, rainfall, and wind velocity and direction (measured 10 m above the ground) were collected daily. Instantaneous photosynthetically active radiation (PAR) profiles were measured every meter with a Licor PAR 4π sensor (LICOR LI-1400, Lincoln, Nebraska, USA) and were used to characterize light extinction coefficients, following Beer Lambert's law. Following Tett et al. (2002), it was assumed that 46% of solar radiation was PAR and these PAR J s^{-1} could be converted to photons s^{-1} with 4.16 μmol photons J^{-1}. Water temperature (0.1 °C of accuracy) and conductance with temperature compensation (1% of reading of accuracy) were measured with a Hydrolab DS5 probe (60 readings min^{-1}). Dissolved nutrients, NO_3 (+NO_2), NH_4, PO_4, and $Si(OH)_4$, were measured using widely used colorimetric methods, according to Aminot and Chaussepied (1983) with a Bran & Luebbe's continuous-flow analyzer (except for ammonium). Reagents for ammonium measurement were added in the field to avoid contamination, and were measured 4 h after returning to the laboratory.

2.3. Biomass

Phytoplankton biomass was measured both as a total sample and after fractionation by serial filtration (Rodriguez and Guerrero, 1994; Marañón et al., 2001; Pesant et al., 2002) on 10 μm nylon-fibre filter and on Whatman GF/C glass-fibre filter, using low vacuum pressure (lower than 100 mbar). Concentration in chlorophyll *a* was determined after extraction in 90% acetone overnight in the dark and at 4 °C, with a fluorometer (TD-700, Turner Designs, Sunnyvale, California, USA) according to Welschmeyer (1994).

2.4. Set-up of the protocol for photosynthetic capacity monitoring, using preliminary results

Carbon incorporation rate was measured ~3 h after sampling at high tide (time needed to return to the laboratory), following the widely used method of Steemann-Nielsen (1952). To adjust light intensities in the incubator, we estimated the average daily PAR received by phytoplankton cells over the well-mixed water column based on previous studies (Jouenne et al., 2007). We considered the water column as well-mixed in accordance with the macro-tidal regime. During this study, temperature differences between surface and bottom never exceeded 0.11 °C in Lingreville-sur-mer and 0.39 °C in Baie des Veys. We calculated the daily PAR received on average by phytoplankton cells over the water column according to Pannard et al. (2007), by integrating the light profile over depth:

$$\bar{I} = \frac{\int_0^H I_o e^{-kz} dz}{H}$$

with H the maximal depth at high tide (m), I_o the surface light availability and k the light extinction coefficient. Incubations were thus conducted in triplicate at four light intensities (0, 43.5, 83.5 and 206.5 μmol photon m^{-2} s^{-1}), which is in accordance with light availability observed during this study. Phytoplankton cells received on average 80.5 μmol photons m^{-2} s^{-1} (daily average), with 112.1 μmol photons m^{-2} s^{-1} upper quartile and 54.4 μmol photons m^{-2} s^{-1} lower quartile. The maximal value observed was 166 μmol photons m^{-2} s^{-1}. Incubations were conducted for 40 min to avoid

photo-acclimation and change of physiological parameters (Lizon and Lagadeuc, 1998a,b). Samples were then filtered on Whatman GF/C glass-fibre filter. Radioactive inorganic carbon was removed by acidification and the radioactive organic carbon was measured by radio-luminescence. Results were then standardized to chlorophyll *a* biomass of the total community, to express photosynthetic capacity in mg C mg chl a^{-1} h^{-1}. Platt's model of photosynthesis was used to determine the physiological parameters to fit the photosynthetic capacity irradiance curves, in particular the light saturated photosynthesis (Platt et al., 1980).

2.5. Phytoplankton community structure

To investigate phytoplankton species composition, 500 mL of water was filtered on polycarbonate filter of 1 μm, using a low vacuum pressure (lower than 200 mbar). Cells were then re-suspended in 2 mL of water and fixed with glutaraldehyde (1% of final volume). Cells were counted following the method described in Jouenne et al. (2005) using light microscopy on Sedgewick-Rafter cells and at least 400 units (individual cells or colonies) were counted for each sample. As toxicity depends on species, *Pseudo-nitzschia* species were identified using Transmission Electron Microscopy.

2.6. Numerical analysis

Variability charts of the physical, chemical and biological parameters were performed using the software JMP5.1 (SAS software; www.jmp.com). Canonical Correspondence Analysis (CCA) was performed for each short-term sampling period, between physical and chemical data, and phytoplankton community structure using the computer program CANOCO 4.5 from Microcomputer Power (Braak and Verdonschot, 1995). This multivariate analysis draw a parallel between the environmental parameters and the species concentration, so that it can associate species concentration change with an environmental driver (Braak, 1986).

3. Results

3.1. Annual to short-term variability of the environmental parameters

Water temperature, nutrient load, and chlorophyll *a* concentrations observed in Lingreville-sur-mer and Baie des Veys during the short-term sampling periods were in accordance with available annual data from IFREMER/Quadrige & RHLN and the SMEL HYDRONOR network (Figs. 2 and 3). On an annual time scale, water salinity was lower in Baie des Veys than in Lingreville-sur-mer, indicating a higher estuarine influence in Baie des Veys (Fig. 3). The two sampling sites have a similar trophic statue and biomass stock, except when considering silicon, which is higher in Baie des Veys than in Lingreville-sur-mer (Fig. 3).

The spring sampling period of Lingreville-sur-mer co-occurred with the annual warming of the water column, leading to a gradual temperature increase of 1.1 °C (Figs. 2 and 4). The autumn sampling

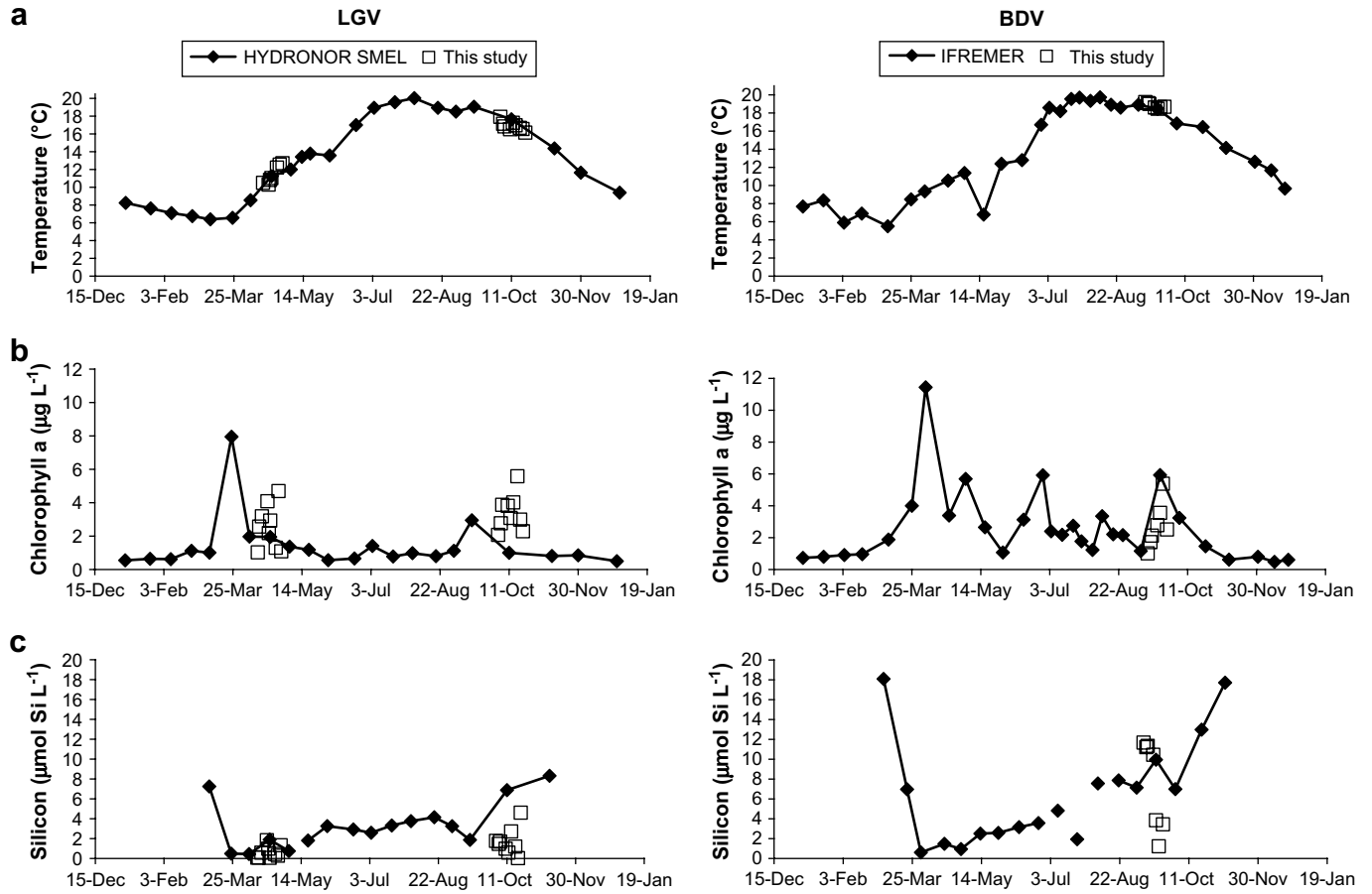

Fig. 2. Annual variation of (a) temperature, (b) chlorophyll *a* and (c) silicon concentration, in Lingreville-sur-mer (left side) and Baie des Veys (right side), observed during both short-term sampling (opened squares) and annual sampling (solid diamonds). "IFREMER" data originate from IFREMER/Quadrige & RHLN and "SMEL HYDRONOR" from Réseau SMEL HYDRONOR.

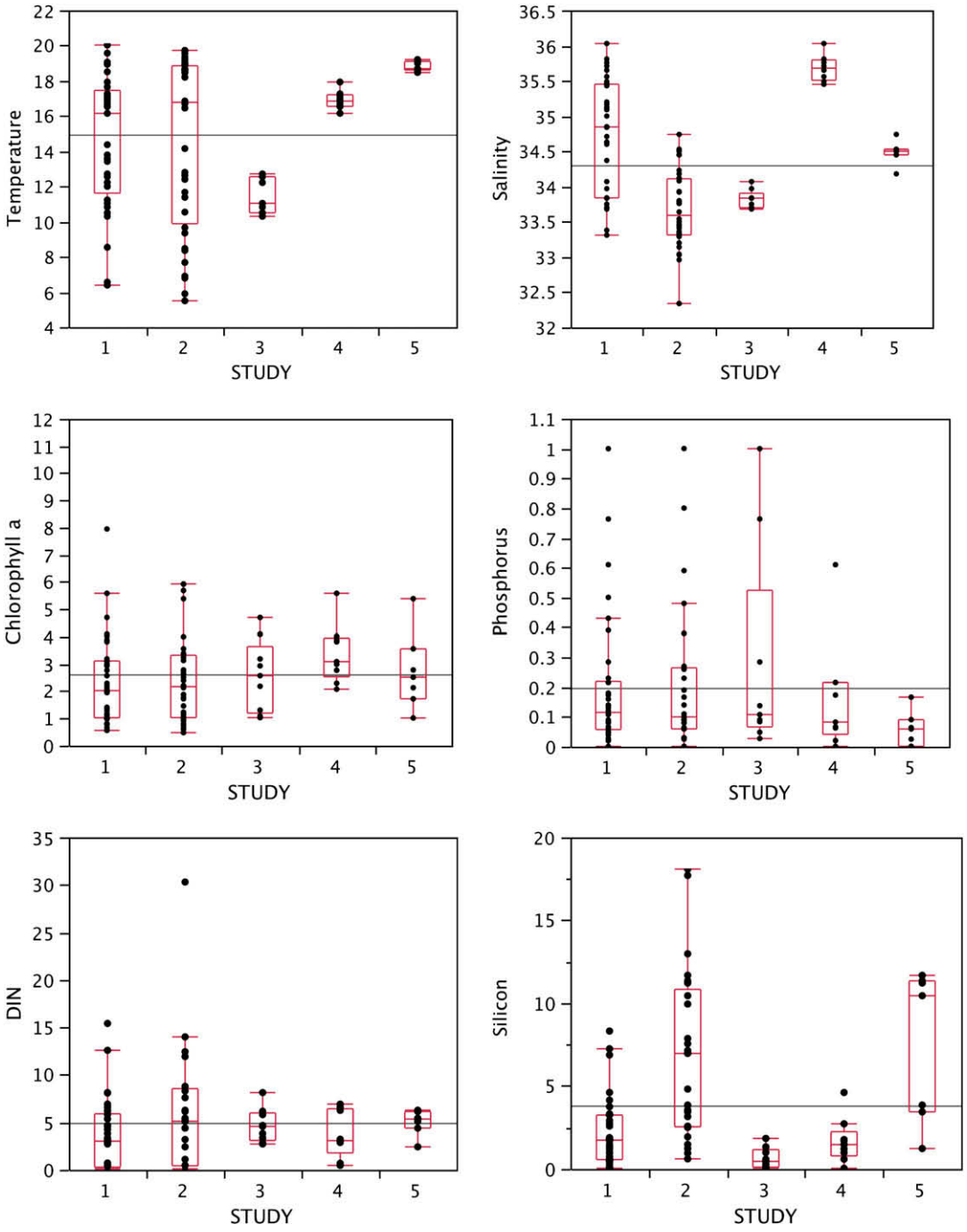

Fig. 3. Annual and short-term variability of physical, chemical and biological parameters: 1: annual variability in Lingreville-sur-mer (IFREMER/Quadrige and IFREMER/RHLN data associated with short-term data); 2: annual variability in Baie des Veys (IFREMER/Quadrige and IFREMER/RHLN data associated with short-term data); 3: short-term data from Lingreville-sur-mer in spring; 4: short-term data from Lingreville-sur-mer in autumn; 5: short-term data from Baie des Veys in autumn.

period of Lingreville-sur-mer was done during the annual cooling of the sea, leading to a gradual decrease of −1.78 °C over the 3 weeks (Figs. 2 and 4f). The autumn sampling in Baie des Veys was performed at the end of the period with maximal temperatures and the temperature slightly decreased during the study by −0.74 °C (Figs. 2 and 4f).

Salinity changed only slightly during each sampling period, with 0.39, 0.58 and 0.56 PSU, respectively, for Lingreville-sur-mer in spring and in autumn, and for Baie des Veys (Figs. 3 and 4e). The short-term variability in salinity was associated with mixing with estuarine waters of lower salinity. Some decreases of salinity, probably linked to these mixing events, were observed during the three sampling periods (Fig. 4e). The decrease was on average 0.3 PSU. Considering a salinity of 35 PSU for the water mass and of 10 PSU for estuarine waters (Jouenne et al., 2007), this mixing event represents an estuarine water input of 1.2 L per 100 L of the water mass. The main possible mixing events were in Lingreville-sur-mer the 19th of April, the 4–5th and 16th of October and in Baie des Veys, the 20th of September (Fig. 4e).

Despite the low short-term variability of temperature and salinity, we observed a high short-term variability in biomass and nutrient concentration compared with annual variability, sometimes half the concentration range observed at the annual scale (Figs. 2 and 3). More than 50% of the biomass range observed at the

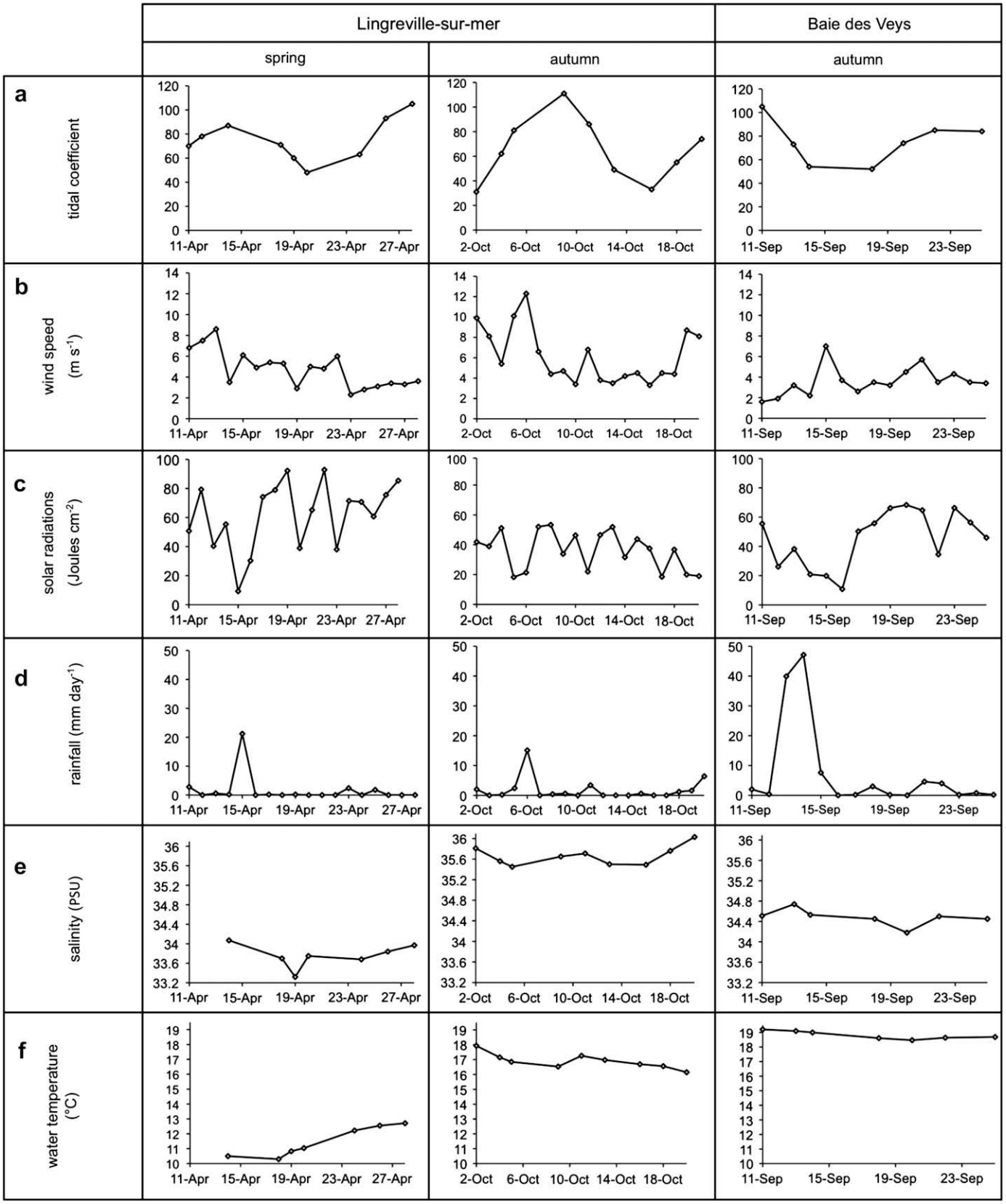

Fig. 4. (a) Tidal coefficient (ratio of the tidal range in any semi-diurnal cycle to the range at the greatest spring tide multiplied by 120), (b) wind speed, (c) solar radiations, (d) rainfall, (e) salinity and (f) water temperature, observed during the three sampling periods, in Lingreville-sur-mer and in Baie des Veys, in spring and in autumn 2006.

annual scale in Lingreville-sur-mer was observed during each 3-week sampling period (Fig. 3). Similarly the silicon concentration during each sampling period represented half of the range observed at the annual time scale in Baie des Veys (Fig. 3). The highest short-term variability was observed for phosphorus in spring in Lingreville-sur-mer and for silicon in autumn for Baie des Veys (Fig. 3).

Nutrient ratios Si:N:P were compared to the Redfield ratio (Si:N:P = 16:16:1) in order to characterize which nutrient was the most likely to become limiting (Fig. 5). Nutrient availability was thus highly variable during each sampling period and all nutrients were potentially limiting at one time during study (Fig. 5). In spring in Lingreville-sur-mer, the nutrient limitation changed temporarily from silicon to phosphorus, between the 18th and the 20th of April (Fig. 5). The concentration in silicon increased by a factor of 2 (Fig. 6c). In autumn, in Baie des Veys, nutrient limitation changed from phosphorus and nitrogen to silicon on the 20th of September (Figs. 5 and 6a–c). During autumn in Lingreville-sur-mer, limitations by silicon and phosphorus alternated, except on the 11th and the 13th of October, when the community was mainly limited by nitrogen (Fig. 6a). Changes in nutrient limitation observed during this study and calculated from nutrient ratios are similar to changes in nutrient limitation calculated from nutrient half-saturation coefficients (as used in Cugier et al. (2005)).

3.2. Annual variability in phytoplankton community structure, photosynthetic capacity, and size-fractionated biomass

Dominant phytoplankton species were mainly diatoms, in accordance with previous studies (Jouenne et al., 2007) and the macro-tidal regime (Cebrian and Valiela, 1999). The succession of dominant species observed by REPHY was similar in Lingreville-sur-mer and Baie des Veys until the beginning of May, with dominance of *Skeletonema* sp. followed by a bloom of *P. globosa* (IFREMER/Quadrige & RHLN and Réseau SMEL HYDRONOR). Dominant species then diverged between the two sites, with *A. glacialis*, *Rhizosolenia delicatula* and *Chaetoceros socialis* dominating in Baie des Veys, and cryptomonads, *R. fragilissima* and *R. delicatula* dominating in Lingreville-sur-mer (IFREMER/Quadrige & RHLN and Réseau SMEL HYDRONOR). From October on, *Skeletonema* sp. dominated both sites, with *A. glacialis* in Baie des Veys and *R. delicatula* in Lingreville-sur-mer (IFREMER/Quadrige & RHLN and Réseau SMEL HYDRONOR). On an annual time scale, the only Harmful Algal Bloom species observed was *P. globosa*.

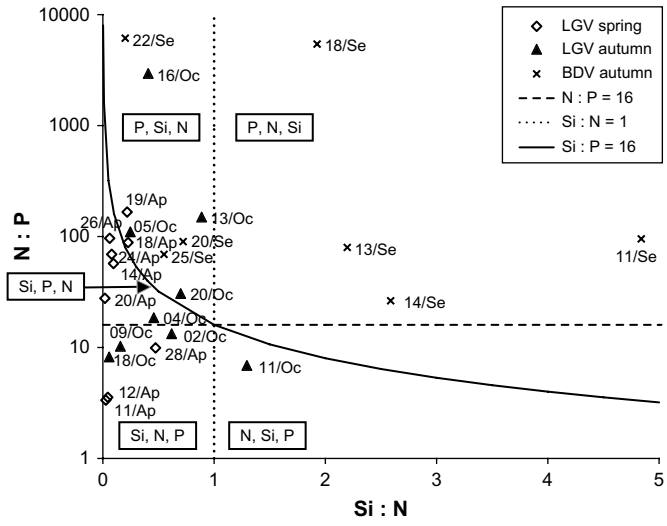

Fig. 5. Synthetic graphic of the Si:N:P ratio in the water column at the different sampling dates (Ap: April, Se: September, Oc: October). Nutrients are given in the order of their limitation for each part of the graph.

The first short-term sampling period in Lingreville-sur-mer was performed during the onset and increase of *P. globosa*, while the autumnal sampling period in Baie des Veys was performed during the dominance of *C. socialis*. The second sampling period in Lingreville-sur-mer was performed during the dominance of *Skeletonema* sp. Finally the succession of dominant species observed during the three short-term sampling periods was *P-n. delicatissima*, *P. globosa* (with cells of *Pseudo-nitzschia* included in *Phaeocystis* colonies) and *A. glacialis* in spring, followed by *Guinardia striata*, *Leptocylindrus danicus*, *C. lorenzianus*, *C. debilis*, *P-n. pungens* and *A. glacialis* in autumn (Fig. 6f). Concentrations of species, however, were lower in autumn, compared with spring. *R. imbricata* remained one of the dominant species during the three sampling periods (Fig. 6f). On a short-time scale, new potentially toxic species were observed compared with annual time scale (*P-n pungens* and *P-n delicatissima*, both identified using Transmission Electron Microscopy).

Photosynthetic capacity in autumn, observed both in Baie des Veys and in Lingreville-sur-mer, was quite similar that measured in Jouenne et al. (2007). Photosynthetic capacity in spring in Lingreville-sur-mer, however, was higher, with high short-term variability (factor of 10 between minimal and maximal values – Fig. 6d). No other photosynthetic capacity data were available in Lingreville-sur-mer to compare with. Low biomass and high photosynthetic capacity thus characterized Lingreville-sur-mer site, particularly during the sampling period in spring with the increase of *P. globosa*.

The chlorophyll *a* biomass of small cells (smaller than 10 μm) fluctuated only slightly both between and during each sampling period (Fig. 6e). Concentration always remained close to 1 $\mu g\,L^{-1}$. The biomass of large cells (larger than 10 μm) changed over time during each sampling period, but did not significantly change between periods (Fig. 6e). The temporal trend followed the pattern of the dominant species, particularly in autumn (Fig. 6e,f).

3.3. Short-term change in photosynthetic capacity, biomass, and community structure

In spring in Lingreville-sur-mer, a shift occurred in the nutrient limitation from silicon for diatoms to phosphorus for every species, between the 18th and the 20th of April (Figs. 5 and 6). The photosynthetic capacity of the entire community, initially dominated by diatoms, followed the same pattern as the silicon concentration (Fig. 7a,b). The biomass of small cells remained the same during the entire study, while the biomass of large cells fluctuated between 1 and 2.5 $\mu g\,L^{-1}$ (Fig. 6e). Following the silicon input and the increase in photosynthetic capacity, the concentration of the two diatoms, *P-n. delicatissima* and *R. imbricata*, increased by a factor of 12.4 and 5.9, respectively, in 6 days (Fig. 6f). This led to a change in the community structure: the communities sampled until the 18th of April can be distinguished from the communities sampled after the 18th, using the first axis of the CCA (Fig. 7c). On the left part of the CCA, the diatoms *P-n delicatissima* and *R. imbricata* characterized the community of the 20th and the 24th of April, while the prymnesiophyte *P. globosa* characterized the community of the 26th and 28th of April (Fig. 7c). *Phaeocystis globosa* increased quickly during this period, so that cellular concentration changed from 50 to 400 cells mL^{-1} (Fig. 6f). From IFREMER data, we know that *P. globosa* increased at least until the 4th of May (IFREMER/Quadrige and IFREMER/RHLN). The rapid increase of *Phaeocystis* coincided with the period of low wind velocity (Fig. 4b), which led to a decrease of the light extinction coefficient (Fig. 7c), in parallel with solar radiation increase (Fig. 4c). The light extinction coefficient was on average 0.67 m^{-1} before the 19th of April, with a maximal value at 1.18 m^{-1} and then

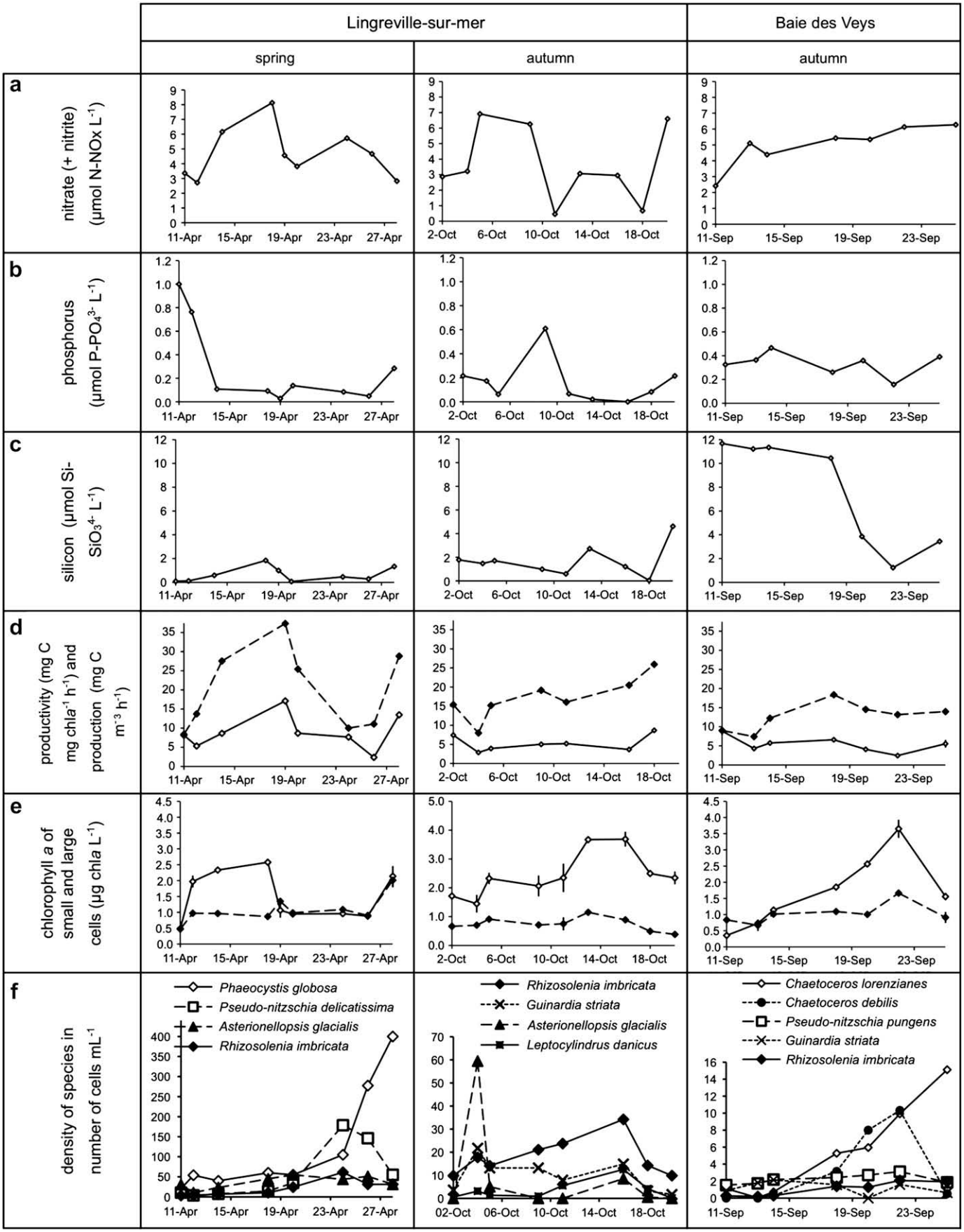

Fig. 6. (a) Nitrate and nitrite, (b) phosphorus, (c) silicon, (d) photosynthetic capacity (solid line with opened diamonds) and production (dotted line with solid diamonds), (e) chlorophyll *a* associated with large (solid line with opened diamonds) and small (dotted line with solid diamonds) cells and (f) concentration of the different species (pay attention to the different scales), observed during the three sampling periods, in Lingreville-sur-mer and in Baie des Veys, in spring and in autumn 2006.

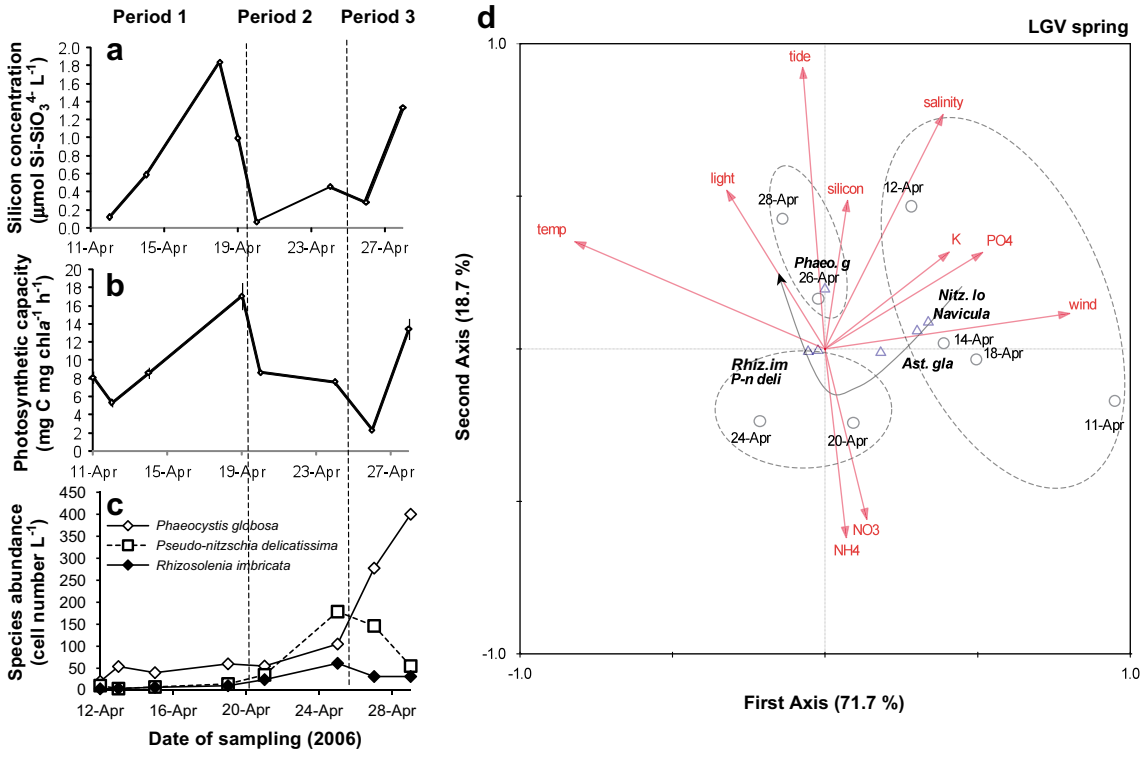

Fig. 7. Temporal patterns in (a) silicon concentration and (b) in photosynthetic capacity. (c) Abundance of three dominant species. (d) Canonical Correspondence Analysis of the community structure in Lingreville-sur-mer, in spring, depending on sampling time (the dotted circles highlight the three main community structures observed during the sampling period and the arrow represents the direction of the change). Species: Ast Gla (*Asterionellopsis glacialis*), Nav (*Navicula* sp.), Nitz lo (*Nitzschia longissima*), Phaeo g (*Phaeocystis globosa*), P-n deli (*Pseudo-nitzschia delicatissima*), Rhiz im (*Rhizosolenia imbricata*). Variables: *k* (light extinction coefficient), tide (tidal coefficient), wind (wind speed), temp (water temperature), salinity (salinity), light (mean light availability in the water column), PO_4 (phosphate), silicon (silicon), NO_3 (nitrate), NH_4 (ammonium).

decreased to 0.275 m^{-1} between the 20th and the 26th of April. Temperature and wind speed are the two environmental parameters that contributed to the first axis of the CCA (Fig. 7c). Tidal coefficient, salinity, ammonium and nitrogen concentrations contributed to the second axis (Fig. 7c). Finally two changes in community structure characterized the spring sampling period in Lingreville-sur-mer. The first change was associated with a silicon input and a higher photosynthetic capacity of the community and led to the increase of *P-n delicatissima* and *R. imbricata*. The second change was associated with the onset of the dominance of *P. globosa*.

In autumn in Lingreville-sur-mer, biomass of small cells remained similar during the study, with concentration lower than 1 µg L^{-1} (Fig. 6e). The biomass of large cells was initially 1.5 µg L^{-1} and increased to 2 µg L^{-1} in parallel with a nitrate increase (from 3.2 to 6.9 µmol N L^{-1}) between the 4th and the 5th of October (Fig. 6a,e). The biomass of large cells increased once again, from 2 to 3.7 µg L^{-1} between the 11th and the 13th of October, in parallel with a new nitrate increase, from 0.5 to 3.1 µmol L^{-1} (Fig. 6a,e). However, the last increase in nitrate concentration (from 0.7 to 6.6 µmol N L^{-1}) between the 18th and the 20th of October was not associated with a change in biomass of large cells (Fig. 6a,e). The phosphorus concentration was also increased by a factor of 10, between the 5th and the 9th of October, from 0.06 to 0.61 µmol P L^{-1} (Fig. 8a). During this period, the photosynthetic capacity rose by 28% (from 3.9 to 5.0 mg C mg chl a^{-1} h^{-1}) and the production by 26% (from 15.2 to 19.1 mg C mg m^{-3} h^{-1}; Fig. 6d). Following the phosphorus input and the increase in photosynthetic capacity, the abundance of two diatoms, *L. danicus* and *R. imbricata*, increased (Fig. 6f). *Rhizosolenia imbricata* thus rose by 62% between the 9th and the 16th of October, while *L. danicus* was increased by a factor of 12.5 (Fig. 6f). Phytoplankton community (sampled the 11th and the 18th) can be distinguished from the other sampled communities using the second CCA axis (Fig. 8). Wind, turbidity, silicon and nitrate were the main environmental factors that contributed to the second axis. Phosphorus did not contribute, maybe due to the time-lag between the nutrient input and population increase (Fig. 8). The first axis of the CCA highlights the phytoplankton community sampled the 4th of October, associated with high concentration of *A. glacialis* (Fig. 8). Light and salinity contributed to this first axis, so that a highlight availability and low salinity water characterized the community of the 4th (Fig. 8). Finally two community changes characterized the sampling period of autumn in Lingreville-sur-mer: the first one associated with a decrease in salinity and an increase in *Asterionellopsis* without a time-lag, and the second one associated with a phosphorus input. The initial community sampled on the 2nd of October was similar to that sampled at the end of the study (the 20th of October), as can be seen by their proximity on the CCA (Fig. 8).

The beginning of the autumnal sampling period in Baie des Veys was characterized by a lower light availability received by cells over the water column (Fig. 9a). The mean light availability until the 16th of September was 28.5 ± 16.0 J µm cm^{-2}, while the mean light availability from the 17th of September was 56.5 ± 11.4 J cm^{-2} (Fig. 9a). Silicon concentration was high during the first period with 11.4 ± 0.2 µmol Si L^{-1}, while it decreased quickly during the second one, with an average 4.7 ± 4.0 µmol Si L^{-1} (Fig. 9b). On the 22nd of September, the silicon concentration became potentially limiting (Figs. 5 and 6c): the maximal photosynthetic capacity was observed the 18th of September, with 18.36 mg C L^{-1} h^{-1}, when the light became high and the silicon concentration was still high (Fig. 6c,d). The photosynthetic capacity followed the same pattern as the silicon concentration, as soon as light became high (Fig. 9b,c). An increase in total biomass was then observed, from 1.19 ± 0.05 µg chl

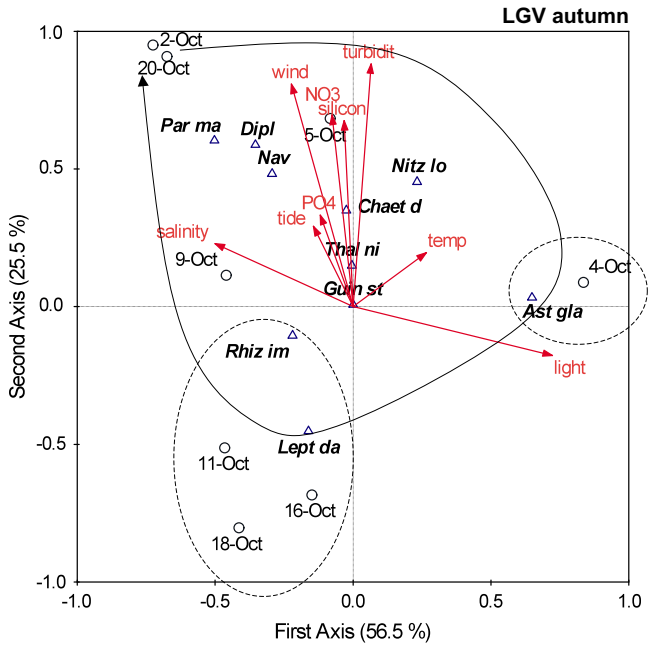

Fig. 8. Canonical Correspondence Analysis of the community structure in Lingreville-sur-mer, in autumn, depending on sampling time (the dotted circles highlight the three main community structures observed during the sampling period and the arrow represents the direction of the change). Species: Ast Gla (*Asterionellopsis glacialis*), Chaet d (*Chaetoceros decipiens*), Dipl (Diploneis sp.), Guin st (*Guinardia striata*), Lept da (*Leptocylindrus danicus*), Nav (Navicula), Nitz lo (*Nitzshia longissima*), Par ma (Paralia marina), Thal ni (*Thalassionema nitzschioides*), Rhiz im (*Rhizosolenia imbricata*). Variables: turbidit (turbidity), tide (tidal coefficient), wind (wind speed), temp (water temperature), salinity (salinity), light (mean light availability in the water column), PO_4 (phosphate), silicon (silicon), NO_3 (nitrate).

$a\,L^{-1}$ on the 11th of September to $5.31 \pm 0.38\,\mu g\,chl\,a\,L^{-1}$ on the 22nd of September (Fig. 9c). Three diatoms, with two dominating the community, followed the same temporal pattern as the biomass, *C. debilis*, *P-n. pungens* and *R. imbricata* (Fig. 6f). These diatoms then decreased as soon as silicon became limiting. Four other diatoms, with two dominating the community, *Chaetoceros lorenzianus*, *R. imbricata*, *Navicula* sp. and *Thalassiosira rotula*, increased in concentration from the light availability increase until the end of the sampling period (Fig. 6f). The CCA highlighted with the first axis a change in the community structure between communities sampled before the 18th of September and those sampled after (Fig. 9c). The community of the 18th is intermediate between the two periods (Fig. 9c). Several environmental factors contributed to the first axis: higher temperature and salinity, associated with high concentration of silicon, characterized the environmental conditions of communities sampled before the 18th of September (Fig. 9c). Stronger wind, associated with higher turbidity, characterized environmental conditions of the communities sampled after the 18th of September (Fig. 9c). Finally a change in community structure was observed associated with a change in light availability and the phytoplankton community induced a decrease in silicon stock during this sampling period.

4. Discussion

4.1. Short-term variability: local processes and mixing of water masses

The coastal water mass is an open system with a high short-term variability in physical and chemical conditions due to mixing processes with surrounding water masses. This high short-term variability may then influence growth and competition among species. In the case where mixing processes dominate over local ones, one could expect to observe a high short-term variability of both physical, chemical, and biological, with changes in phase occurring the same day. During the three periods of sampling, changes in temperature and salinity remained small, indicating a low influence of mixing processes in freshwater compared with local processes. There were few sudden changes in population concentrations, except for the species *A. glacialis*. *Asterionellopsis glacialis* was observed throughout the year, with higher concentration in spring during which this species commonly dominates the community (Rousseau et al., 2002). *Asterionellopsis glacialis* is an estuarine species (Jouenne et al., 2007), and, in autumn, freshwater inputs were identified through the increase in concentration of this species. Mixing events in autumn were thus characterized in this study by an increase of *A. glacialis* in parallel with a decrease in salinity, as highlighted by the CCA for the sampling date of the October 4th in Lingreville-sur-mer. Both changes occurred without time-lag, unlike for local processes. Similarly, several increases in biomass were associated with an increase in nitrate in the water column occurring without time-lag and could also be related to a mixing event.

In the case where local factors mostly influenced the dynamics of the phytoplankton community, the short-term variability in physical and chemical factors should be followed by changes in the biological parameters after a time-lag. Nutrient stock and light availability were the main environmental drivers that influenced phytoplankton community structure on a short-time scale, in accordance with previous studies on different time scales (Egge and Aksnes, 1992; Pennock and Sharp, 1994; Rousseau et al., 2000). Changes in community structure observed after a time-lag of a few days were considered as being induced by local processes.

An increase in nutrient the most limiting for growth induced an increase in photosynthetic capacity. Time-lags before the onset of cell division varied between a few minutes to 24 h depending on species strategy, depending upon growth response versus storage response (Collos, 1986). Photosynthetic capacity thus showed a high variability during sampling periods, with on average a factor of 3.3 between minimum and maximum values observed during the sampling period. This increase in photosynthetic capacity was followed by an increase in population concentration after a time-lag of a few days. The time-lag thus changed with the biological parameters we were interested in, being as small as a few hours for photosynthetic capacity to as large as a few days for the community structure, as observed in lakes (Pannard et al., 2008). The population increase ended with the occurrence of a new limitation by nutrient or light. We twice observed such modification of the community structure in response to nutrient input, in Lingreville-sur-mer in spring and in autumn, following silicon input and phosphorus input, respectively.

An increase in light availability in nutrient-replete conditions can also induce a community change. In autumn in Baie des Veys, photosynthetic capacity increased when light availability increased and silicon stock was high. Biomass then increased, decreasing silicon stock until it became potentially limiting. The community structure also changed in favor of *Chaetoceros* species (*C. lorenzianus*, *C. debilis* and *C. socialis*) and *R. imbricata*. Light availability may also have influenced the non-siliceous species, *P. globosa*, in Lingreville-sur-mer in spring. This species releases a significant amount of dimethyl sulphide, which is an important climate-cooling aerosol (Verity et al., 2007). Blooming success of *Phaeocystis* is partly explained by its ability to form gel-like colonies, creating an energy and nutrient reservoir (Schoemann et al., 2005). Annual spring blooms of *P. globosa* were observed in the eutrophicated coastal areas of the North Sea (Cadée, 1996) and generally follow the diatoms spring bloom. Several hypotheses are advanced in literature. *Phaeocystis* develops in silicon-depleted conditions,

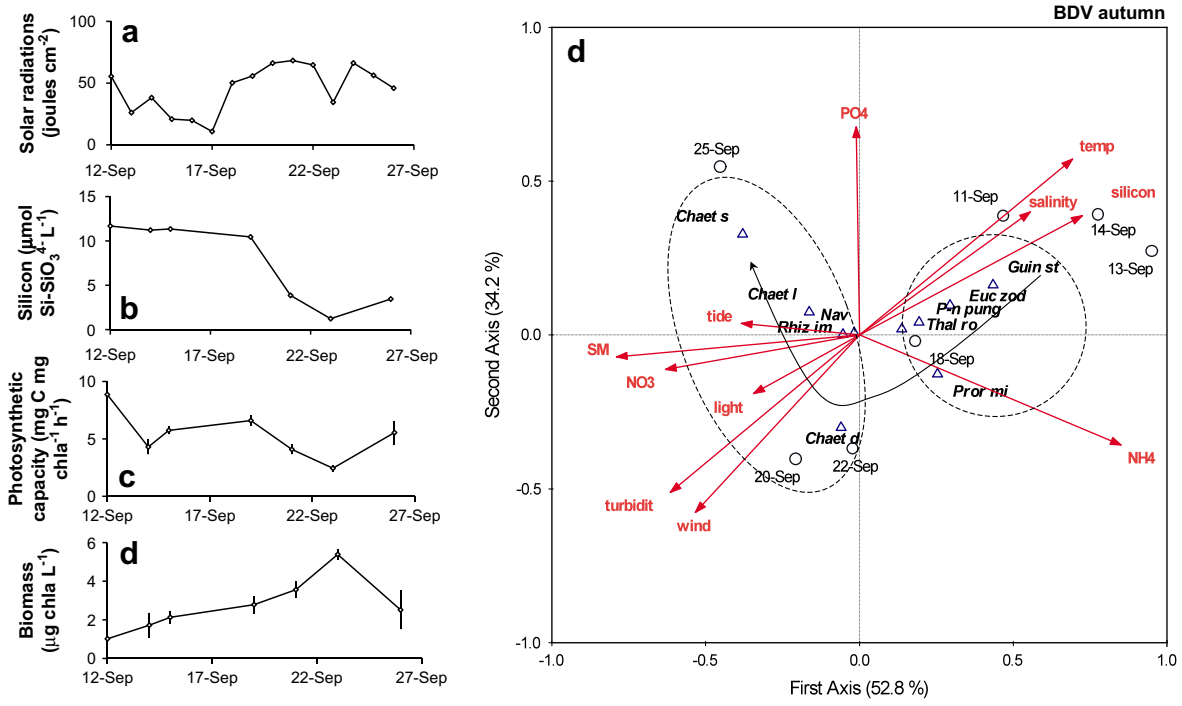

Fig. 9. Temporal pattern in (a) solar radiations, in (b) silicon concentration and in (c) photosynthetic capacity (dotted line) and biomass (solid line) of the total community, in Baie des Veys, in autumn. (d) Canonical Correspondence Analysis of the community structure and the environmental parameters depending on sampling time (the dotted circles highlight the three main community structures observed during the sampling period and the arrow represents the direction of the change). Species: Chaet d (*Chaetoceros decipiens*), Chaet l (*Chaetoceros lorenzianus*), Chaet s (*Chaetoceros socialis*), Euc zod (*Eucampia zodiacus*), Guin st (*Guinardia striata*), Nav (*Navicula* sp.), Pror mi (*Prorocentrum micans*), P-n pung (*Pseudo-nitzschia pungens*), Rhiz im (*Rhizosolenia imbricata*), Thal ro (*Thalassiosira rotula*). Variables: SM (suspended matter), turbidit (turbidity), tide (tidal coefficient), wind (wind speed), temp (water temperature), salinity (salinity), light (mean light availability in the water column), PO_4 (phosphate), silicon (silicon), NO_3 (nitrate), NH_4 (ammonium).

while diatoms have a competitive advantage over *Phaeocystis* in silicon-repleted conditions, due to the higher growth rate and the higher storage ability of diatoms (Egge and Aksnes, 1992, MEPS; Escaravage et al., 1995). But spring blooms of *P. globosa* develop when light and temperature are higher. Light, nutrients, and water temperature are thus the main factors controlling the growth and biomass of the colonial form (Whipple et al., 2005). Other environmental factors were also demonstrated to control the growth of *P. globosa* (e.g. vitamin B12 and iron (Peperzak et al., 2000)). In this study, while diatoms were influenced by the silicon input, colonies of *P. globosa* increased in density at the end of the sampling period, when wind and light extinction coefficients were the lowest and light was high. *Phaeocystis* blooms seemed to be influenced by light in this study, in accordance with previous studies (Peperzak et al., 1998). Factors like vitamin B12 were not tested here.

4.2. Time scales of local processes and mixing of water masses

Resulting from this study two major scales of community change can be distinguished: instantaneous community changes associated with mixing events, and delayed community changes associated with a change in light or nutrient availability. Previous work also highlighted these two major scales of community change in a small reservoir (Harris and Trimbee, 1986). The first scale of 1 day was associated with horizontal advection of water within the basin, while the second scale (between 5 and 14 days) was associated with growth and biological restructuring of the community. On a annual time scale, time-lag between environmental change and biological response can be neglected, as the time-lag, which varies between a few minutes to a few days, is small compared with the rate of sampling.

Such increase in photosynthetic capacity and biomass has already been observed following a meteorological event or a water discharge when associated with a nutrient input on a short-time scale. Arin et al. (2002) observed an increase in biomass and a change in community structure following a nutrient upwelling event in the Western Alboran Sea. A wind mixing event in the Northwestern Mediterranean Sea induced an increase of flagellates and diatoms during a few days in the sub-surface zone (Bustillos-Guzman et al., 1995). Further, it was shown in Galveston Bay estuary, that nitrogen pulsing events can rapidly increase diatom biomass and thus change the phytoplankton community structure (Örnólfsdóttir et al., 2004). Similarly in Chesapeake Bay, an ammonium input due to a wind-driven mixing induced an increase of photosynthetic capacity and biomass and a bloom occurred after a few days (Yeager et al., 2005). Short-term variability of the phytoplankton community in coastal ecosystem was thus already highlighted (Côté and Platt, 1983), but strong mixing events or nutrient upwelling events are not necessary to induce changes in community structure, as demonstrated in this study. Even if local processes still dominate over mixing, short-term variability of both community structure and biological parameters can be observed and can occur more frequently than expected. Short-term variability in the hydrographical and biological features was observed by Madariaga (2002) in a shallow temperate estuary. The author observed a bloom of the cryptophyceans *Euglena* sp. and the dinoflagellate *Peridinium foliaceum*, with the improvement of weather conditions, particularly light (Bay of Biscai). Lastly, it can be important to characterize short-term phytoplankton dynamics, as they can reduce the accuracy of predictive models of seasonal succession (Côté and Platt, 1983). As explained in Harris and Trimbee (1986), succession can be viewed as a "series of allogenic perturbations followed by biological restructuring of the community".

A successional episode, as well as the presence of toxic species, may be missed by a bi-weekly sampling rate. In Lingreville-sur-mer

in autumn, we observed a reversion to the initial community structure after 18 days. This reversion was not associated with the spring/neap tidal cycle. Returns to earlier stages of the succession in the phytoplankton community were previously observed in a tropical lake, by Lewis (1978), who observed series of successional episodes generally initiated by nutrient inputs. The high irregularity of nutrient supply may explain the reversions. This return to the initial community raises the issue of the sampling schemes and the need to better understand the short-term dynamics of coastal phytoplankton. Moreover, shellfish may accumulate toxins over a few days. Mussels, for instance, can accumulate domoic acid produced by *Pseudo-nitzschia* at a maximal rate of between 0.21 and 3.7 $\mu g\ DA\ g\ DW^{-1}\ h^{-1}$, with a depuration rate of domoic acid at about 17% d^{-1} (Wohlgeschaffen et al., 1992). Considering an accumulation rate of 1 $\mu g\ DA\ g\ DW^{-1}\ h^{-1}$ and a legal limit of 20 $\mu g\ DA\ g\ DW^{-1}$, mussels farming will be forbidden after only 24 h. In our study, population increases due to local process were observed during a period of 5–7 days, such as the potentially toxic species *P-n delicatissima* in spring. Finally even if we can't exclude totally the hypothesis that several consecutive mixing events induced similar changes on similar time scales, sudden mixing events may be distinguished from gradual changes of the phytoplankton communities associated with the local factors. Many questions are still opened, but satellite imagery, tools for continuous data acquisition and novel molecular tools may be combined together to provide new insight into the duality between the two time scales of changes, the local processes and the mixing processes.

5. Conclusion

Fluctuations of biomass, as well as the concentration of estuarine species like *A. glacialis*, were influenced by mixing events, while delayed community structure changes were influenced by local processes. Short-term variability in physical and chemical forcing influenced the dynamics of coastal phytoplankton communities when it was associated with a change in light or nutrient limitation. The biological response, measured as photosynthetic capacity, occurred after a time-lag of a few hours, while the modifications of the community structure occurred after a time-lag of a few days. The increase in density of a toxic species may easily be missed through a bi-weekly sampling, leading to difficulties in linking shellfish poisoning with *in situ* phytoplankton communities.

Acknowledgement

This study was supported by the Conseil Régional de Basse-Normandie, the Agence de l'Eau-Seine-Normandie, Laboraroire Départemental Franck Duncombe (Conseil Général du Calvados), the Syndicat Mixte pour l'Equipement du Littoral (Conseil Général de la Manche) and the Centre de Recherche en Environnement Côtier (UCBN, Luc-sur-Mer). We also specially thank Stéphane Pacary, Bertrand Bouchaud and Jean-Louis Blin (Lingreville-sur-mer) and Philippe Hérisson, Frédéric Guyot and Alain Savinelli for the (Baie des Veys). Valérie Bouchard from LDFD and Didier Goux from the Centre de Microscopie Electronique are thanked too. Radioactive experiments were performed in the Laboratoire de Manipulation des Radio-Eléments (UCBN). We are also grateful to people who helped with field work, laboratory analysis or species identification: Chantal Billard, Ian Probert, Mathieu Vimard, Nathalie Josselin and Marie-Paule Briand. We also thank Rich Vogt (UQAM) for advice and the English correction and the two anonymous reviewers for their useful comments on the manuscript.

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