Long-term hydrological and phytoplankton monitoring (1992–2007) of three potentially eutrophic systems in the eastern English Channel and the Southern Bight of the North Sea

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The spatial and main temporal variations in nutrient concentrations and phytoplankton abundance were investigated between 1992 and 2007 in the eastern English Channel and the Southern Bight of the North Sea, zones of consistent presence of *Phaeocystis globosa* and diatom blooms. Silicate and phosphate were the main nutrients potentially limiting phytoplankton growth, but the dynamics of the limitation seemingly differ between sites. Phosphate concentration showed a clear monotonic decreasing trend, whereas dissolved inorganic nitrogen and silicate trends were more complex. Nitrate was rarely or never a limiting factor. Results highlight three main periods with a *Phaeocystis*- or diatom-dominated system in the 1990s, and a more complex pattern in the 2000s. The composition of the phytoplanktonic community is described and an attempt made to establish a link between the community and its environment in terms of variability, shifts, and trends. The effects of larger- vs. regional-scale controlling factors are also discussed.

Keywords: diatoms, eastern English Channel, eutrophication, long-term series, *Phaeocystis globosa*, Southern Bight of the North Sea.

Introduction

Monitoring the quality of marine waters is essential to better understanding, and therefore better management, of the coastal environment, leading to sustainable development and utilization of the resources. The coastal zone plays a key role in biogeochemical cycles by supporting biological productivity, as well as for anthropogenic activities carried out in its vicinity. Eutrophication is probably one of the best-known of the consequences of human activities that threaten the health of many coastal areas. It is a process driven by the enrichment of water by nutrients, especially compounds of nitrogen and/or phosphorus, leading to increased growth, primary production and biomass of algae, changes in the balance of organisms, and degradation of water quality. The consequences of eutrophication are undesirable if they lead to appreciably degraded ecosystem health and/or unsustainable provision of goods and services (OSPAR Commission, 2009). Processes of eutrophication involve changes in inorganic nutrient load and light availability as a consequence of increasing biomass, and these are the main environmental factors influencing phytoplankton growth.

A long-term increase in anthropogenic input of nitrogen loads in the coastal waters of most developed countries has been observed over recent decades, whereas the management of

Europe's watersheds since the 1980s has resulted in a reduction in river loadings of phosphate (Claussen *et al.*, 2009). These regime shifts in nutrients induced changes in phytoplankton productivity and biomass (Cadée and Hegeman, 2002), as well as in its composition. There has been a shift in dominance from siliceous (diatoms) to non-siliceous (and often toxic flagellate) species (Del Amo *et al.*, 1997).

In the shallow, well-mixed temperate coastal waters of the eastern English Channel and Southern Bight of the North Sea, where the thermocline does not persist and the water column is well mixed (Gentilhomme and Lizon, 1998), regular and intense blooms of the foaming and noxious *Phaeocystis globosa* have been recorded regularly (Schapira *et al.*, 2008). These areas are under the direct influence of two eutrophic systems (the bay of Seine and some parts of the North Sea), as well as from local continental tributaries (Lacroix *et al.*, 2007). *Phaeocystis* sp. blooms are suspected to be controlled mainly by nutrients (Lancelot *et al.*, 1998).

Much of the work on long-term dataseries has highlighted the fact that the patterns of phytoplankton limitation are closely linked to local hydrography and hydrology (Loebl *et al.*, 2009). Some authors have investigated the spatial distribution of nutrients between the French and English coasts or the seasonal variations

in nutrients during limited (and sometimes atypical) periods (e.g. Gentilhomme and Lizon, 1998; Schapira et al., 2008), but we are unaware of any long-term studies dealing with a global overview of nutrient dynamics in the eastern English Channel and the Southern Bight of the North Sea. However, an attempt was made to investigate a potential link between the interannual variability of P. globosa blooms in the area and climate (Irigoien et al., 2000; Seuront and Souissi, 2002). For Belgian coastal waters of the North Sea, Breton et al. (2006) highlighted large-scale climatic features (such as the North Atlantic Oscillation) interacting with the local meteorological and hydrographical conditions that drive phytoplankton dynamics.

Ifremer's regional nutrient monitoring programme (SRN, Suivi Régional des Nutriments) has since 1992 provided a database of nutrients and phytoplankton observations in French coastal waters of the eastern English Channel and the Southern Bight of the North Sea. According to the national implementation of the European Water Framework Directive (WFD 2000/60/CE) and the framework of the second application of the Common Procedure of the Oslo and Paris Convention (OSPAR; http://www.ospar.org/) of 2007, the results of the SRN have been integrated into a database that is used to define the ecological status of the water masses in terms of eutrophication (Claussen et al., 2009).

Within this environmental and legal context, this paper consists of a description of the main spatial and temporal distributions of nutrients and phytoplankton at three sites in northern French coastal waters of the eastern English Channel and the North Sea during the first 16 years of monitoring of the SRN network. The main aims of the work are to define the seasonal and spatial distributions and to explore major interannual trends in variability of both nutrient concentrations and phytoplankton blooms. Evidence for regime shifts is also sought. The work will hopefully facilitate evaluation in the long term of the effectiveness of ongoing watershed management plans, in particular with regard to eutrophication issues.

Material and methods
Sampling sites and strategies

The English Channel is characterized by a macrotidal regime (tidal range ~3 and ~9 m during neap and spring tides, respectively, in the Straits of Dover) that generates fast tidal currents essentially parallel to the coast and a northeast-flowing tidal residual current from the English Channel to the North Sea. Along the French coast, fluvial supplies from the Bay of Seine to Cap Gris-Nez generate a coastal water mass that drifts nearshore, separated from the open sea by a frontal area (Brylinski and Lagadeuc, 1990). Exchanges between inshore and offshore water masses (the transportation of particles and nutrients) depend basically on the tide and are more notable during the neap than during the spring tide. This may seem counterintuitive, but during the neap tide, the frontal structure between inshore and offshore waters is more inclined from the vertical, resulting in a greater surface for exchange between coastal and offshore waters, and leading to enhanced exchange possibilities between the two water masses (Brylinski and Lagadeuc, 1990).

Three sampling areas along an inshore–offshore transect were investigated by Ifremer between 1992 and 2007 within the framework of SRN, two located in the eastern English Channel, (i) off Boulogne-sur-Mer (next to the Straits of Dover), a coastal zone separated from the open sea by a frontal area, and (ii) in the Bay of Somme, the second-ranked estuarine system after the Seine estuary on the French coasts of the English Channel, and another area located in the Southern Bight of the North Sea, i.e. (iii) off Dunkerque harbour, a shallow well-mixed coastal zone (Figure 1). The main environmental characteristics of the areas are listed in Table 1.

Sample analysis

Water samples were collected subsurface using a 5-l Niskin bottle twice per month from March to June and monthly during the rest of the year. The methodologies used for chlorophyll a, ammonia, nitrite, nitrate, phosphate, and silicate analysis are outlined in Aminot and Kérouel (2004). Chlorophyll a concentrations were estimated by spectrophotometry after filtration through glassfibre filters and extraction in 90% acetone.

An accurate test of nutrient limitation requires a detailed measurement of algal growth under experimental nutrient addition (D'Elia et al., 1986). Nonetheless, to determine potential limitation of primary production by nutrient availability, the standard molar ratio for dissolved inorganic nitrogen (DIN = ammonium + nitrite + nitrate), phosphate, and silicate was calculated and compared, using Redfield et al. (1963) and Brzezinski (1985) as references for the composition of biogenic matter (Si:N:P = 16:16:1).

Phytoplankton samples were preserved in acid lugol, then subsamples of 10 ml were settled for 24 h in a counting chamber according to the method of Ütermöhl (1958). Cell enumerations were made by inverted microscopy within a month of sample collection to preclude significant changes in phytoplankton size and abundance. Except for Phaeocystis enumeration, >400 phytoplankton cells in each sample were counted with a 20× Plan Ph1 0.5NA objective, resulting in an error of 10%. For counting P. globosa, only the total number of cells was computed. A minimum of 50 solitary cells was enumerated from several fields chosen randomly (10–30) with a 40× Plan Ph2 0.75NA. The abundance of cells in a colony was determined using the relationship between colony biovolume and cell number defined by Rousseau et al. (1990).

Data analysis

The statistical analyses applied here are explained in Legendre and Legendre (1998). A cumulative function (Ibanez et al., 1993) was applied to the hydrological data to detect the general trends in variations. For a chronological series of data $x(t)$, sampled at time t and varying between 1 and N, the reference value k is the mean k. After subtracting k from all data, we successively added the residuals and obtained

$$St = \sum_{i=1}^{t} xi - tk. \tag{1}$$

This cumulative function (reported as s-values on the right axis of figures hereafter) is highly sensitive to changes in the mean value of the series. The local mean between two points is equal to the slope of the curve between those two points, plus the reference value k: for successive data equal to k, the curve would be horizontal, and for successive values lower than k, the slope would be negative, and vice versa.

Two methods were employed jointly to allow interpretation of dominance of the different phytoplankton groups or taxa. To help
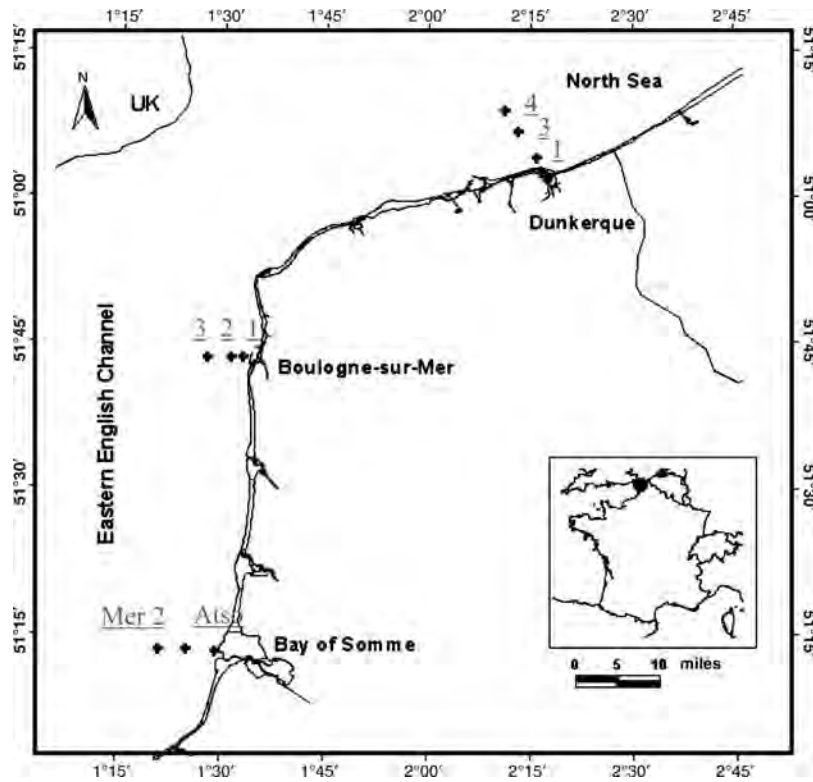
Figure 1. Location of the sampling stations (SRN network) along the French coast in the eastern English Channel (Bay of Somme and Boulogne-sur-Mer) and in the Southern Bight of the North Sea (Dunkerque).

Table 1. Main environmental characteristics of the three ecosystems, Dunkerque, Boulogne-sur-Mer and the Bay of Somme.

Characteristic	Dunkerque macrotidal (shallow water, <30 m)	Boulogne-sur-Mer macrotidal (under the influence of a frontal structure)	Bay of Somme macrotidal (estuary with medium turbidity)
Main river	Aa	Liane	Somme
Length (km)	89	37	263
Watershed (km^2)	1 215	244	6 550
Mean river flow (m^3 s^{-1})	10	3	35

define the temporal structure of the coastal phytoplankton community, a matrix analysis was carried out [date × log (total abundance of cells per litre + 1)]. The date groups were calculated by the method of flexible bonds, using the algorithm of Lance and Williams (Legendre and Legendre, 1998) with the specific coefficients $\alpha = 0.625$, $\beta = -0.25$, and $\gamma = 0$. To take variations in abundance of taxa in the samples being compared into account, the quantitative distance index of Bray–Curtis was used:

$$B_{j,k} = \frac{\sum_{i=1}^{n} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{n} (Y_{ij} - Y_{ik})}, \qquad (2)$$

where Y_{ij} and Y_{ik} are, respectively, taxon i abundance in samples j and k.

The biological index of a species is the cumulative total of ranks occupied by that species on all the dates on which it was counted. The rank of a species on a given date is a function of its dominance relative to other species. The biological index was calculated according to the method of Sanders (1960). For each date, species were classified according to their abundance. The most abundant, and therefore the most dominant on a given date, was given the value of 10. Hence, ten species were classified for each date. For each species, the scores obtained on all dates were added and their sum corresponded to the Sanders index. Guille (1970) proposed the following biocenotic classification of species according to the Sanders index, for a given site:

(i) species classified in the first ten rows are referred to as preferential species for that site;

(ii) species classified in the following ten rows are referred to as the accompanying species of that site;

(iii) species for which the Sanders index is zero are referred to as accessories of that site.

The diversity index revealed the main composition of the phytoplanktonic community at the level of a taxonomic class, and hierarchical clustering allowed us to identify different periods where such classes dominated the ecosystem.

Results

Main characteristics and seasonal patterns of variability in nutrients and chlorophyll *a*

The maximum and the mean or median concentrations of chlorophyll *a*, DIN, and silicate (maxima, respectively, 58.5 µg l^{-1},

60.0 µmol l^{-1}, and 35.2 µmol l^{-1} in the Bay of Somme, with comparable but lower values for Dunkerque) decreased from the Bay of Somme and Dunkerque sites towards Boulogne-sur-Mer, where the values were at their least. Phosphate concentration mean and maximum values decreased from north to south, from Dunkerque (maximum ~10 µmol l^{-1}) to no more than ~3 µmol l^{-1} at the Boulogne-sur-Mer and Bay of Somme coastal stations (Figures 2–4).

Although seasonal cycles were well defined on all transects, there were no differences in timing along coastal-offshore gradients (data not shown). Consequently, only the results from coastal stations are presented in Figures 2–4. Chlorophyll a concentrations began to rise in late winter (February), then remained high from March to June (Figures 2–4), with maxima in April at all three sites. At Boulogne-sur-Mer, they only reached 30 µg l^{-1} in April. In the Bay of Somme and off Dunkerque, maximum chlorophyll a values >50 µg l^{-1} were recorded in April. After a summer of lower concentrations (often <10 µg l^{-1}), there was a slight increase in September.

DIN median concentrations (20–30 µmol l^{-1}; Figures 2–4) dropped suddenly between March and April, then decreased to levels close to the detection limit of <0.15 µmol l^{-1}, in summer. Concentrations then increased from September in the Bay of Somme, and more progressively from October at the Boulogne-sur-Mer and Dunkerque sites, before reaching levels comparable with those of the previous winter. The seasonal pattern of phosphate and silicate concentrations (Figures 2–4) was relatively similar for the three sites. Concentrations of both nutrients were high between November and February (median values >1 and >10 µmol l^{-1}, respectively, for phosphate and silicate), then dropped to minima in April, sometimes to levels close to the detection limit, respectively, <0.05 and <0.10 µmol l^{-1}. Concentrations of both rose again in summer (Dunkerque and Boulogne-sur-Mer) or autumn (Bay of Somme).

Changes in macronutrient concentration influenced the stoichiometric ratios. Figure 5 delimits six areas, each characterized by potentially limiting nutrients, in the order of priority [according to the boundaries for biogenic particles defined by Redfield et al. (1963) and Brzezinski (1985): Si:N = 1, N:P = 16, and Si:P = 16]. By pooling all available nutrient data from the period 1992–2007, it would appear that silicate was potentially the major limiting nutrient throughout the year at Boulogne-sur-Mer and Dunkerque (Table 2), followed by (i) P-limitation from January to April and October to December, and (ii) N-limitation from May to September (Figure 6). In the Bay of Somme, P:Si:N and Si:P:N limiting orders of priority coexisted (Table 2). At that site, the Si:N:P limiting orders of priority were less frequent (16% of data) over the whole time-series than for the other two sites (>30% of the data). Consequently, for the Bay of Somme, nitrogen was rarely, if ever, the limiting factor during the growth season.

Long-term coastal station dataseries of nutrients and chlorophyll a

In coastal waters off Dunkerque, chlorophyll a and DIN concentrations have gradually decreased since the 1990s, according to the parabolic shape of the cumulative function (Figure 2). Chlorophyll a concentrations were particularly high (>25 µg l^{-1}) in 1993, 1994, 1996, 1999, 2001, and 2007. No trend is visible in the shape of the cumulative function for silicate concentration. Phosphate concentrations were particularly high in

1993, 1995, and 2005 (>>2 µmol l^{-1}), with a slightly decreasing trend over the study period (Figure 2).

In coastal waters off Boulogne-sur-Mer, chlorophyll a concentrations peaked (>20 µg l^{-1} in 1994, 2000, and 2003; Figure 3). The positive slope of the cumulative function indicates that chlorophyll a concentrations were globally higher for the period 1998–2007 than earlier (Figure 3). Further, DIN concentrations were regularly less from the start of the 2000s than the averaged concentration over the period 1992–2007. Phosphate concentration decreased over the whole period, but silicate concentration increased gradually over the whole period (Figure 3).

In the Bay of Somme, chlorophyll a concentrations were higher from the end of the 1990s. High concentrations (>40 µg l^{-1}) were recorded in 1994, 1995, and 1997, and from 1999 to 2002 (Figure 4). DIN concentrations were globally higher in the 1990s, but then declined (<40 µg l^{-1} from the start of the 2000s; Figure 4). Phosphate concentrations were low (maxima ~1 µmol l^{-1}) from the end of the 1990s and in the 2000s except for 2005 and 2006. Silicate concentrations seemed to evolve cyclically, with values higher in 1994 and 1995, then decreasing and subsequently increasing in the early 2000s, followed by another decrease from 2002 (Figure 4).

Aside from phosphate concentrations, which declined overall at the three sites over the period 1992–2007, interannual evolution of DIN and silicate concentrations was more complex and seemed to consist of major shifts rather than regular reductions or increases (Figures 2–4).

The change in the N:P ratio was different between the three sites, as shown by comparing the three nutrient curves per site (Figures 2–4). The decrease in phosphate concentration probably fuelled higher N:P ratios between 1995 and 1997, whereas increased occasional DIN loads would have resulted in high N:P ratios between 2004 and 2007 at the Dunkerque site. The ratio was high from 1999, concomitant with an increase in DIN loads at Boulogne-sur-Mer. The decrease in phosphate concentration resulted in high N:P ratios in 1995, 1996, 2000, and 2001 in the Bay of Somme, before the large decrease there in DIN concentration. The Si:N ratio was generally higher from 2003 at the three sites. The Si:P ratio increased considerably in 1995, 1997, and 2004 at Dunkerque, and in 2000, 2001, and 2005 in the Bay of Somme. That ratio has appeared to increase regularly since the beginning of the study, or at least since 2001, for the Boulogne-sur-Mer site.

Phytoplankton abundance and composition

Of the taxa sampled during the period 1992–2007, Bacillariophyceae (diatoms), Prymnesiophyceae, Dinophyceae, and Cryptophyceae were the main components of phytoplankton communities (Figure 6), and Chlorophyceae, Chrysophyceae, Dictyochophyceae, Raphidophyceae, and Prasinophyceae represented just minor groups in terms of abundance. Based on the Sanders index, calculated annually for the whole period 1992–2007, the taxa regularly considered as dominant were P. globosa (Prymnesiophyceae), the diatoms Chaetoceros sp., Thalassionema nitzschioides, Paralia marina, and some species of Guinardia (Guinardia striata, Guinardia delicatula) and the associated Rhizosolenia imbricata. The diatom Skeletonema costatum completed the list of dominant taxa at the Dunkerque and Boulogne-sur-Mer sites, whereas Asterionellopsis glacialis, Leptocylindrus sp., and Pseudo-nitzschia seriata supplemented the list in the Bay of Somme. For all transects, the accompanying

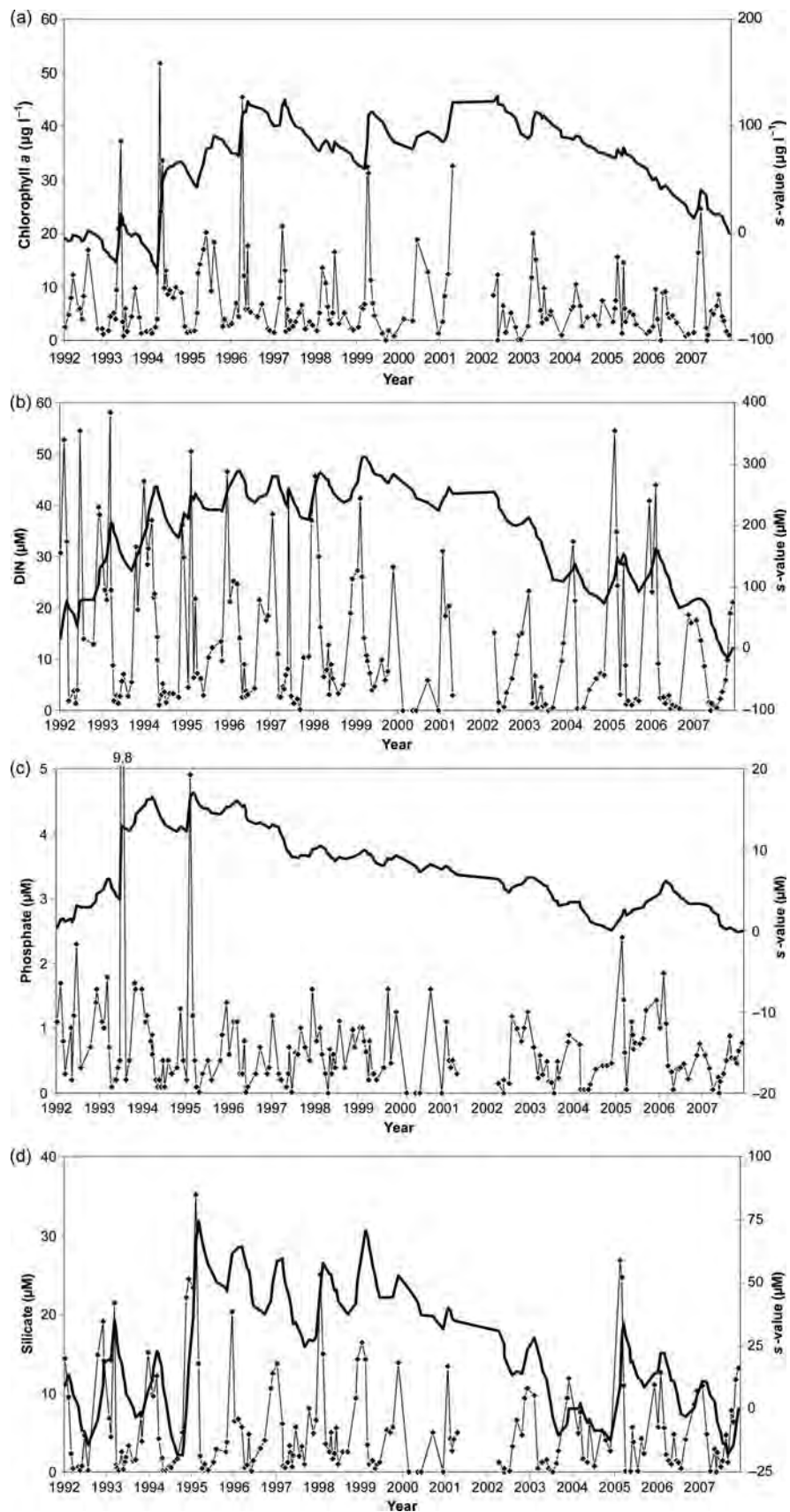**Figure 2.** Temporal distribution (1992–2007) of (a) chlorophyll *a* concentration (μg l^{-1}), (b) DIN concentration (μmol l^{-1}), (c) phosphate concentration (μmol l^{-1}), and (d) silicate concentration (μmol l^{-1}) at the coastal station off Dunkerque and the associated cumulative function (heavy black line). The right-axis values correspond to *s*-values in the same units as the parameters considered.
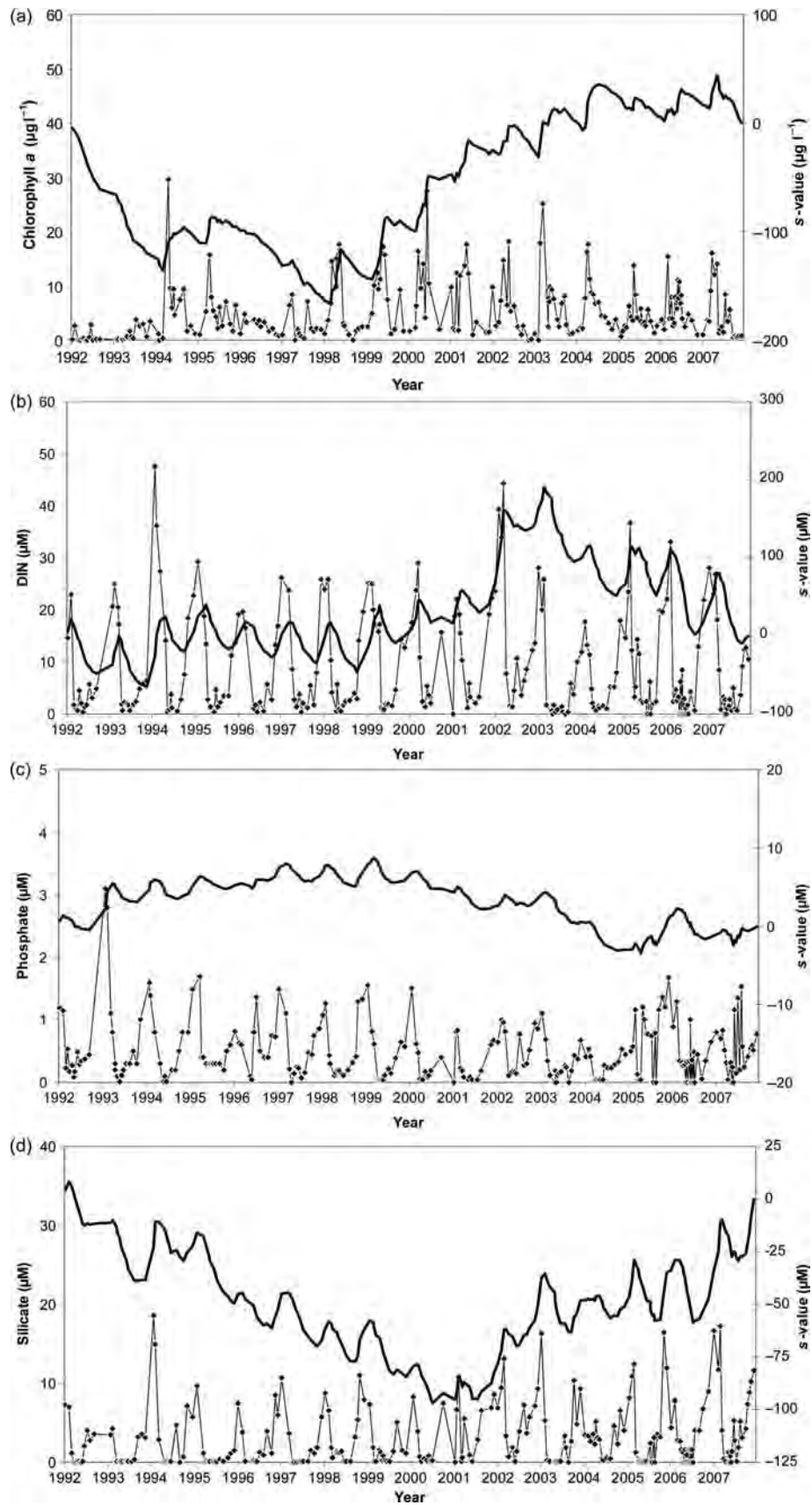
Figure 3. Temporal distribution (1992–2007) of (a) chlorophyll *a* concentration (μg l^{-1}), (b) DIN concentration (μmol l^{-1}), (c) phosphate concentration (μmol l^{-1}), and (d) silicate concentration (l^{-1}) at the coastal station off Boulogne-sur-Mer and the associated cumulative function (heavy black line). The right-axis values correspond to *s*-values in the same units as the parameters considered.

Figure 4. Temporal distribution (1992–2007) of (a) chlorophyll *a* concentration (μg l^{-1}), (b) DIN concentration (μmol l^{-1}), (c) phosphate concentration (μmol l^{-1}), and (d) silicate concentration (μmol l^{-1}) at the coastal station off the bay of Somme and the associated cumulative function (heavy black line). The right-axis values correspond to *s*-values in the same units as the parameters considered.
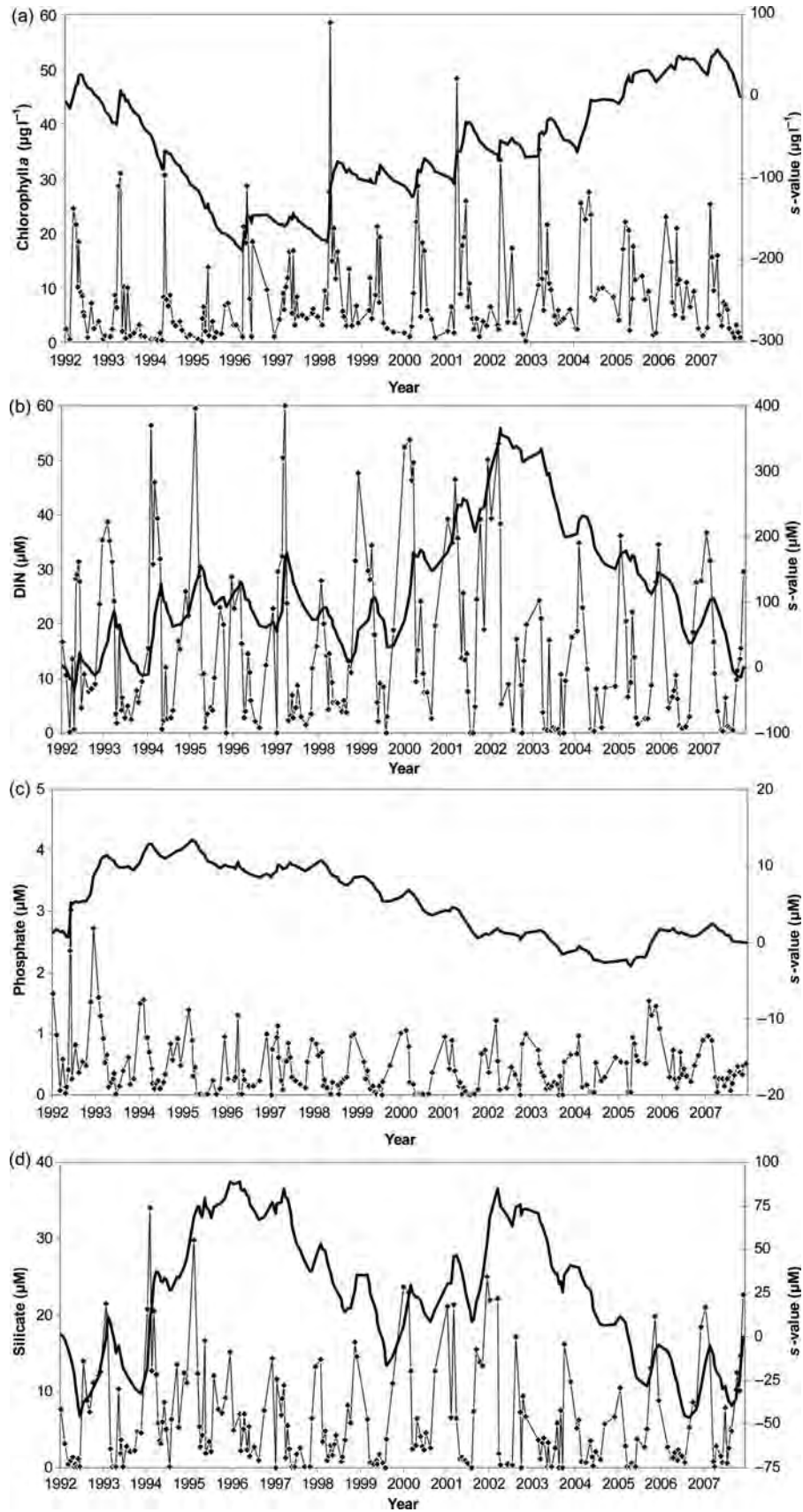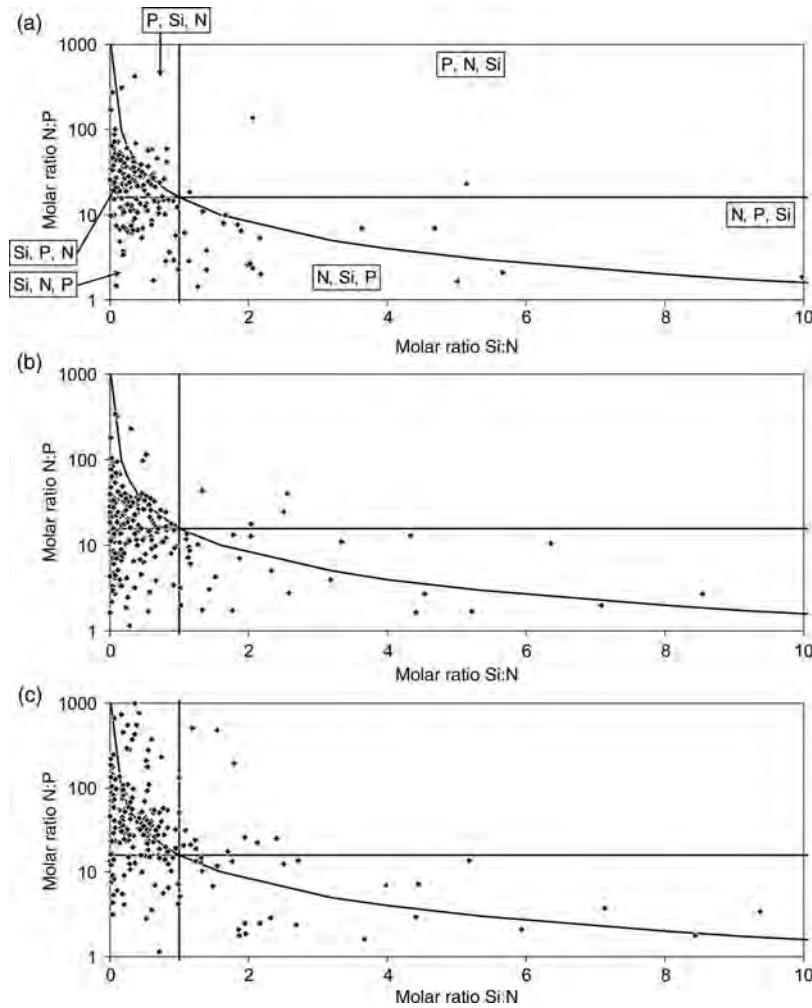
Figure 5. Synthetic graph of Si:N:P molar ratios from 1992 to 2007 at (a) Dunkerque, (b) Boulogne-sur-Mer, and (c) the Bay of Somme. As illustrated for (a), each area is delimited by ratios and shows the potential limiting order of priority.

Table 2. Percentage of occurrence of the main potential limiting nutrients (nitrate, phosphate, or silicate, by order of priority) for the three coastal stations during the period 1992–2007.

Site	P:Si:N	Si:P:N	Si:N:P	n
Dunkerque	10.4	41.5	32.8	183
Boulogne	6.6	41.6	36.7	226
Bay of Somme	33.0	32.6	16.1	218

n, total number of computed data.

species were the diatoms *Chaetoceros socialis*, *Guinardia* sp., *Lauderia* sp., species of the genera *Thalassiosira* (*Thalassiosira* sp. and *Thalassiosira rotula*) and *Pseudo-nitzschia* (*Pseudo-nitzschia* sp. and *P. seriata*; dominant in the Bay of Somme) and the associated *Nitzschia longissima*; the dinoflagellate *Gymnodinium* sp., and some Cryptophyceae.

Phytoplankton peaked always at coastal stations of the three sites, and abundance was higher at the Bay of Somme site than at either Boulogne-sur-Mer or Dunkerque. *Phaeocystis globosa* was the main contributor to phytoplankton total abundance, with greater concentrations generally at coastal stations (Table 3). Concentrations were highest in the Bay of Somme

($>48.10^6$ cells l^{-1}), next highest off Dunkerque (with high concentrations inshore and offshore: up to 28×10^6 and 22×10^6 cells l^{-1}, respectively), and lowest off Boulogne-sur-Mer (decreasing from inshore to offshore, with maximum values of 29×10^6 and 8×10^6 cells l^{-1}, respectively).

Temporal patterns of the main phytoplankton groups

Patterns of phytoplankton abundance revealed strong seasonal and interannual variability at the three coastal sites (Figure 7). At Dunkerque, total abundance ranged from $\sim 10^3$ to $\sim 4 \times 10^6$ cells l^{-1} in the mid-1990s, reaching values $>28 \times 10^6$ cells l^{-1} at the end of that decade (in 1999). Total abundance decreased to $<10^4$ cells l^{-1} at the start of the 2000s, before rising again at the end of the sampling period ($>14 \times 10^6$ cells l^{-1}). Abundance at the Boulogne-sur-Mer site was below the 1992–2007 mean during the 1990s, with maximum values around 10×10^6 cells l^{-1}. In the early 2000s, the range was between 10^3 and $>29 \times 10^6$ cells l^{-1}. Phytoplankton abundance was highest in the Bay of Somme, where maximum values increased between 1992 and 2001, reaching up to tens of million cells per litre. In the 2000s, however, abundance was lower than the 1992–2007 mean.
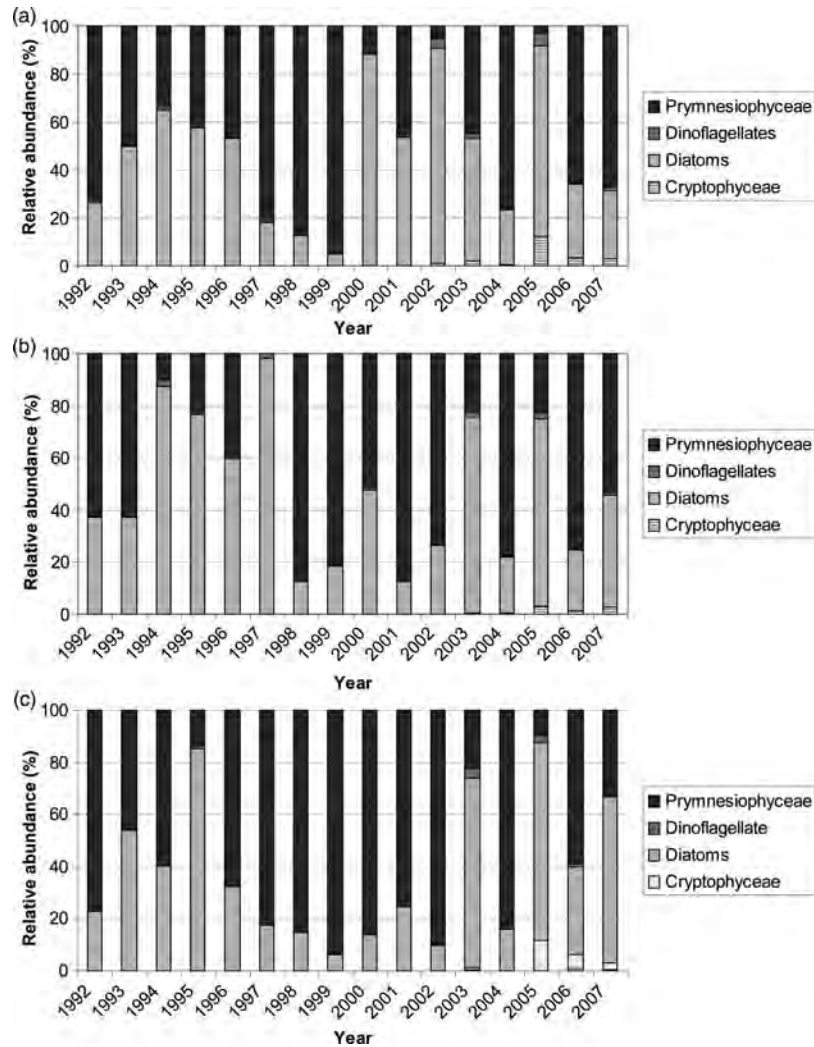
Figure 6. Relative proportion of the main phytoplankton groups (expressed as a percentage of annual total abundance) during the period 1992–2007 at the coastal stations off (a) Dunkerque, (b) Boulogne-sur-Mer, and (c) the Bay of Somme.

Table 3. Minimum, mean, median, maximum, and first (Q1) and third (Q3) quantiles of the total abundance of *P. globosa* (cells l^{-1}) for each station during the period 1992–2007 (*n*, number of computed data).

Parameter	Dunkerque 1	Dunkerque 3	Dunkerque 4	Boulogne-sur-Mer 1	Boulogne-sur-Mer 2	Boulogne-sur-Mer 3	Atso	Mer 2
Minimum	500	1 500	6 402	2 250	400	1 330	1 000	3 000
Q1	102 900	54 000	28 800	68 270	28 270	23 125	104 000	129 400
Mean	3 248 667	2 330 827	2 653 913	2 446 989	1 764 897	933 377	4 732 894	3 710 762
Median	772 740	361 960	225 000	516 700	225 000	163 300	651 000	803 500
Q3	3 219 250	1 896 000	2 824 000	1 800 975	1 442 600	926 812	5 576 000	3 990 000
Maximum	28 233 000	1 488 000	22 032 000	29 850 000	12 290 000	8 932 400	48 932 800	3 639 600
n	44	53	45	70	63	55	77	69

The relative contribution of diatoms and *P. globosa* was characterized by strong interannual variability, as shown in Figure 6 for the coastal stations at each site over the whole period. Shifts in dominance patterns were similar at the three sites: the relative contribution of diatoms peaked at the beginning of the 1990s, whereafter diatoms were replaced progressively by *P. globosa* at the end of the decade, then by fluctuating taxonomic dominance during the 2000s. The relative contribution of *P. globosa* was of longer duration at the Bay of Somme site, where the Prymnesiophyceae contributed >50% of the total abundance more frequently (11 years of 16) at the coastal site.

To corroborate and/or to confirm the interpretation of variability patterns, a cluster analysis resulting from hierarchical classification according to the Bray–Curtis index was implemented.
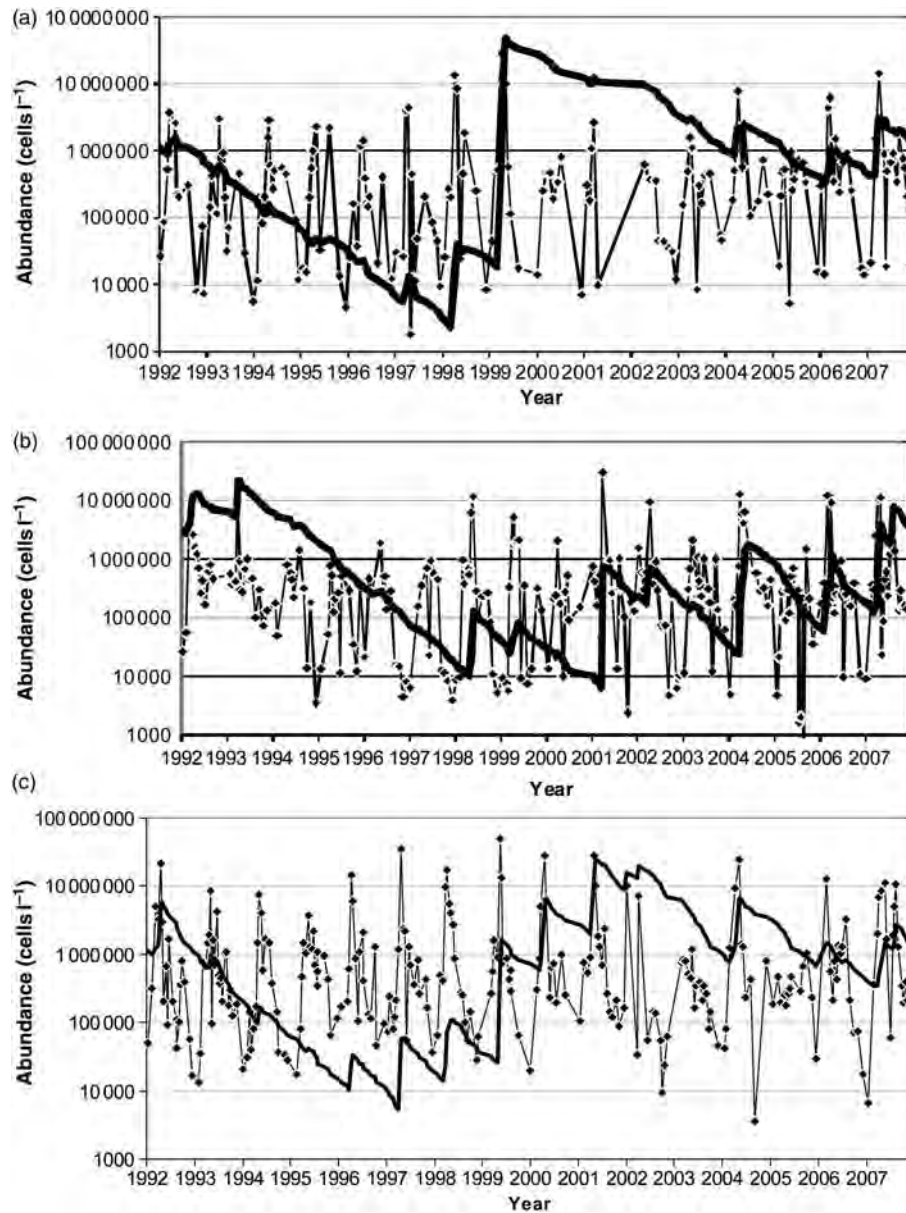
Figure 7. Total phytoplankton abundance (cells l^{-1}) during the period 1992–2007 at the coastal stations off (a) Dunkerque, (b) Boulogne-sur-Mer, and (c) the Bay of Somme and the associated cumulative function (heavy black line).

Table 4. *Phaeocystis*-dominated, diatom-dominated, or intermediate (both *Phaeocystis*- and diatom-dominated) years according to the Bray–Curtis quantitative index calculations for each station during the period 1992–2007.

Station	*Phaeocystis*-dominated system	Diatom-dominated system	Intermediate system
Dunkerque 1	1992, 1997–1999, 2004, 2006, 2007	2000, 2002, 2005	1993–1996, 2001, 2003
Dunkerque 3	1995, 1997–1999, 2003, 2004, 2006, 2007	2000, 2002, 2005	1992–1994, 1996, 2001
Dunkerque 4	1993, 1995–1999, 2004, 2006, 2007	1992, 2000, 2002,	1994, 2001, 2003, 2005
Boulogne-sur-Mer 1	1998, 2001, 2004, 2006, 2007	1994–1997, 2000, 2003, 2005	1992, 1993, 1999, 2002
Boulogne-sur-Mer 2	1995, 1998, 1999, 2001, 2002, 2004, 2006, 2007	1996, 1997	1992–1994, 2000, 2003, 2005
Boulogne-sur-Mer 3	1998, 2004, 2006, 2007	1996, 1997, 2000	1992–1995, 1999, 2001–2003, 2005
Atso	1992, 1997–2001, 2004	1995, 2003, 2005	1993, 1994, 1996, 2002, 2006, 2007
Mer 2	1992, 1998–2002, 2007	2005	1993–1997, 2003, 2004, 2006

That facilitated the highlighting of three types of year dominated by different phytoplankton communities (Table 4). The first type was dominated by diatoms, the second by *P. globosa*, and the third was an intermediate situation when diatoms are important and *P. globosa* was present but with relatively low abundance, and/or specific blooms of another taxon were detected (e.g. Cryptophyceae; Table 4). The Dunkerque site was dominated by *P. globosa* from 1997 to 1999 and in the 2000s, and years dominated by diatoms alternated with intermediate years and with years dominated by *Phaeocystis*. At the Boulogne-sur-Mer site, *Phaeocystis*-dominated years were more frequent in the 2000s, but still alternated with other taxa, especially at intermediate and offshore stations, with diatom-dominated and intermediate periods. At the Bay of Somme site, the dominance of *P. globosa* was particularly evident at the end of the 1990s and at the start of the 2000s, at both stations, before entering a period of alternating years of dominance of diatoms and Prymnesiophyceae (Table 4).

There are some discrepancies in these patterns between stations of a given transect, however, but such observations were probably a statistical artefact or perhaps even spatial heterogeneity.

Discussion

The results of this study have emphasized the importance of long-term site-specific monitoring to detect interannual variability in complex phytoplankton and nutrient biogeochemical cycles in coastal areas subject to anthropogenic influence. Our strategy on the multiscale approach needed to define, model, and predict the effects of anthropogenic eutrophication and climate change on phytoplankton community structure and function was in line with the recommendations of Zingone *et al.* (2010). Our results do underscore the difficulty in defining a general common conceptual framework, above the spring-bloom paradigm (Cloern and Jassby, 2010), to explain the multiscale control of the hydrology and the phytoplankton community.

The marine coastal ecosystems studied, near the Straits of Dover and in the Southern Bight of the North Sea, are at the confluence of the Bay of Seine and the North Sea; both systems are highly sensitive to water-quality change and eutrophication processes (Lancelot *et al.*, 2006; Lacroix *et al.*, 2007; Philippart *et al.*, 2010; Zingone *et al.*, 2010). Strong hydrodynamic conditions (high mixing rate, low residence time) should preserve them from severe eutrophication, but cities and industrial harbours near the Dunkerque and Boulogne-sur-Mer sites, intensive use of fertilizers on the cultivated fields around Boulogne-sur-Mer and the Bay of Somme, and direct estuarine input into the Bay of Somme, all play a key role in the eutrophication.

Lancelot *et al.* (2009) defined a threshold of 4×10^6 cells l^{-1} above which *P. globosa* would disturb the functioning of an ecosystem. In our study, all three sampling sites regularly showed concentrations above this threshold, especially in the Bay of Somme. Moreover, *P. globosa* blooms at all three sites were regularly at concentrations of $>10^6$ cells l^{-1}, considered as the level that indicates eutrophication problems within the framework of the criteria defined by OSPAR for the protection of the marine environment of the Northeast Atlantic (OSPAR Commission, 2009).

The dominance of one species over others can have dramatic effects on planktonic and benthic ecosystem structure and functioning (Lancelot and Rousseau, 1994), leading to severe environmental (Lancelot *et al.*, 1987) and biogeochemical (Wassman, 1994) consequences. The periods when *P. globosa* dominated the phytoplankton community varied from site to site, but so-called "*Phaeocystis* years" occurred at the end of the 1990s at Dunkerque and between the late 1990s and early 2000s at the Bay of Somme, both extended periods of dominance of this prymnesiophyte. At Boulogne-sur-Mer, such dominance was recorded, but did not last for more than the two consecutive years, and there was greater interannual variability, especially in the 2000s. However, there has still been more-frequent dominance of *P. globosa* there (in terms of abundance) since the late 1990s.

Although Gomez and Souissi (2008) recorded a decline in *Phaeocystis* spring blooms from 1998 to 2005 in response to a general trend of de-eutrophication in the North Sea, our dataset revealed a slight decrease in *P. globosa* in the mid-2000s, but high-abundance years alternating with years of lesser abundance at the end of the total period considered. Therefore, general trends calculated over 16 years provide insights into the interannual evolution and maintenance of the blooms.

We are aware of the weakness of our global almost "ataxonomic" approach, but to take the analysis further, extra data mining is needed, but that was not possible within the aims of the present study. Moreover, a taxonomic approach would be limited by the sampling strategy used. Indeed, with full life cycles lasting just a few days, any study of phytoplankton dynamics at a species level would fail under a monthly or at best bimonthly sampling frequency of the SRN monitoring network. In the same area (slightly north of the Boulogne-sur-Mer transect) and with greater sampling frequency, Guiselin (2010) showed that the Reynolds' model (Reynolds *et al.*, 2002) could explain the structure of the phytoplankton assemblages. An approach similar to that of Margalef (1978) was taken in that study, and a combination of nutrient availability and mixing rate of the water column (acting upon light availability) was used to explain the succession of assemblages encountered. The model considered the presence of functional groups, characterized by their physiological and morphological properties, interacting with various regimes of productivity and water mixing, irrespective of seasonal patterns and of the phylogenetic origin of the phytoplankton taxa considered.

At a seasonal scale and on a long-term basis, the present results confirmed that the main nutrients followed a typical temperate cycle, accumulating in winter and decreasing through phytoplankton uptake during spring productivity. Thereafter, a long less-productive period in summer was followed by an autumn and winter period of consolidation (as shown for 1993 in the area by Gentilhomme and Lizon, 1998). Despite the high concentrations of nutrients in winter and the fact that in well-mixed water, regenerated nutrients would be transported upwards into the euphotic zone continuously, nitrate was almost completely consumed between March and April so may have been at limiting concentrations in late spring and summer. In contrast, phosphate concentration dropped to a low level early in spring, explaining the phosphate limitation in these areas then. Looking at changes in the N:P ratio, which are negatively anomalous in summer, our results confirm the conclusions of earlier studies (carried out yearly) in the area (Gentilhomme and Lizon, 1998; Schapira *et al.*, 2008), particularly stressing the importance of nitrate depletion in late spring.

Lancelot *et al.* (2009) showed that a transfer of production within the trophic network too can be related to an imbalance between the inputs of DIN and of dissolved inorganic phosphorus (DIP), which they explained in terms of the more-efficient reduction in the input of DIP than of DIN, the latter remaining

high. Therefore, a ratio of N:P >25 in a system dominated by *P. globosa* would lead to a dominance of colonial forms and a less-effective transfer of production up to higher trophic levels. Applied to our dataseries, we conclude that all stations and sites considered could be disturbed by *P. globosa* between March and May (and later), when the N:P ratio regularly exceeds 25.

Several studies (De Galan *et al.*, 2004; Van der Zee and Chou, 2005) have shown continuously increasing or decreasing trends for DIN, phosphate, and silicate concentrations in the North Sea or other ecosystems over recent decades (Camargo and Alonso, 2006; Loyer *et al.*, 2006; Llope *et al.*, 2007), and our SRN dataseries allows us to highlight the general decrease in phosphate concentrations and more complex changes for DIN and silicate concentrations as a result of the phosphate-reduction practice since the 1970s. DIN concentrations were high, especially in the Bay of Somme, where values peaked at >30 μM in the 1990s. At Dunkerque, DIN dropped throughout the sampling period, and in the Bay of Somme and Boulogne-sur-Mer, it decreased during the 2000s. Although silicate is supposed to remain constant because it is influenced not by human activity but rather through the chemical weathering of silicate minerals (Van der Zee and Chou, 2005), some general changes in its concentration were observed at all three sites, perhaps attributable to freshwater input. However, evaluation of these hypotheses is difficult because of an upstream system controlled by a number of dams or channels, especially for the Boulogne-sur-Mer and Dunkerque sites, and because of a hydraulic system under groundwater influence in the Bay of Somme.

In relation to the Redfield *et al.* (1963) and Brzezinski (1985) ratios that illustrate the annual evolution of potential nutrient limitation, the present results show that an Si:P:N order of limitation commonly at the three sites. Silicate is the main limiting nutrient for Boulogne-sur-Mer and Dunkerque, with phosphate the second most-limiting nutrient from January to April and from September to December, and nitrate a limiting nutrient from May to September. In the Bay of Somme, silicate and phosphate are the main limiting factors, at least potentially. Nitrogen is rarely considered as potentially limiting there, whereas at Boulogne-sur-Mer and to a lesser extent at Dunkerque, the Si:N:P order of limitation is found regularly. A massive uptake of silicate by diatoms leads to its decline, and it then becomes a limiting element for those taxa. The Bay of Somme ecosystem is essentially limited by both silicate and phosphate, the large quantities of nitrate being discharged from the River Somme River preventing nitrogen limitation. More generally, our dataseries suggests that phosphate would limit primary production in the southern North Sea and that nitrogen would likely be limiting in the northern North Sea.

Examination of the nutrient ratios alone does not allow definitive conclusions to be drawn about true limiting nutrients for algal growth, because limitation depends on the species composition and the kinetic curves as well as on the regeneration rates of each nutrient (Del Amo *et al.*, 1997; Loyer *et al.*, 2006). An additional, confirmatory approach to determining nutrient limitation would require comparison of *in situ* nutrient concentrations with the half-saturation constant (K) for nutrient uptake, but it would not allow precise conclusions on limitation patterns because the values reported in the literature for natural populations cover a wide range. For marine species, half-saturation constants apparently vary from 1 to 2 $\mu mol\,l^{-1}$ for DIN, from 0.1 to 0.5 $\mu mol\,l^{-1}$ for phosphate, and from 1 to 5 $\mu mol\,l^{-1}$ for silicic

acid (Escaravage *et al.*, 1999). In our study, concentrations of phosphate were frequently under or near the threshold of 1 μM and followed a south-to-north gradient from the Bay of Somme (lower) to Dunkerque (higher values).

An approach that consists of determining potential major limiting nutrient concentrations needs to take into account the fact that nitrogen limitation could be biased by not having taken into account the DIN such as urea (Gentilhomme and Lizon, 1998) that can be used as a source of nitrogen by phytoplankton. On the other hand, phosphate limitation might be misinterpreted owing to its fast biological and geochemical turnover and its reactivity with suspended matter. The phosphate concentration might be underestimated if its particulate fraction is not considered. Processes of adsorption/desorption of phosphate from the sediment are likely to influence the concentration of dissolved phosphorus in the water column (Loquet *et al.*, 2000). On the other hand, phosphate limitation can be overwhelmed by exo-enzymatic alkaline phosphatase activities that are known to be an effective uptake route for phosphorus in phytoplankton species such as *P. globosa*; such activity has been shown to be important in the field during phosphate-limitation periods (Lamy *et al.*, 2009; Van der Zee and Chou, 2005).

Notwithstanding, nutrient status is not the only factor contributing to a better understanding of phytoplankton phenology and changes in community structure. In the shallow coastal areas of northern Europe, phytoplankton growth is controlled by light and nutrient colimitation (Loebl *et al.*, 2009). In several areas, light-limitation effects exceed those of nutrients (Colijn and Cadée, 2003) and consequently act upon phytoplankton phenology (Iriarte and Purdie, 2004). Some factors, including light and nutrients, were proposed by Peperzak *et al.* (2000) to explain the onset of *P. globosa* blooms in the North Sea. Unfortunately, the current SRN monitoring strategy (low frequency, and a restricted list of environmental parameters) do not allow further investigation of these hypotheses.

In terms of the NAO winter index (December–March), Irigoien *et al.* (2000), Seuront and Souissi (2002), and Breton *et al.* (2006) made some assumptions about its influence on the dynamics of *P. globosa* and/or diatom blooms. Their conclusions seem to be relevant, taking into consideration their time-series, but they are not validated by the present dataset. Instead of considering the annual value and the subsequent pattern of the bloom, we focused on the highly negative values in 1996 and 2001 in the 1992–2007 winter NAO index time-series. This allowed us to recognize three distinct periods for phytoplankton. The first corresponds to years during which *P. globosa* does not dominate the ecosystems, the second to periods of dominance of *P. globosa* over diatoms, and the third to periods of dominance of *P. globosa* over diatoms, but reciprocally not well defined. This last period is characterized by very different types of dominance and bloom dynamics from year to year.

The extreme variability of the third period (after 2000/01) compared with the general situation during the first two periods may be explained by a modification of the balance between large-scale control (at Atlantic and North Sea levels) and regional control (from watershed to coastal zone). This apparent regime shift, which could change the dynamics of triggering factors (e.g. freshwater nutrient and Atlantic inputs, wind effects) is clearly observed in the river run-off series of the Bays of Seine and Somme (Figure 8). Although the interannual magnitude of river flows seems not to have been modified, the frequency seems to
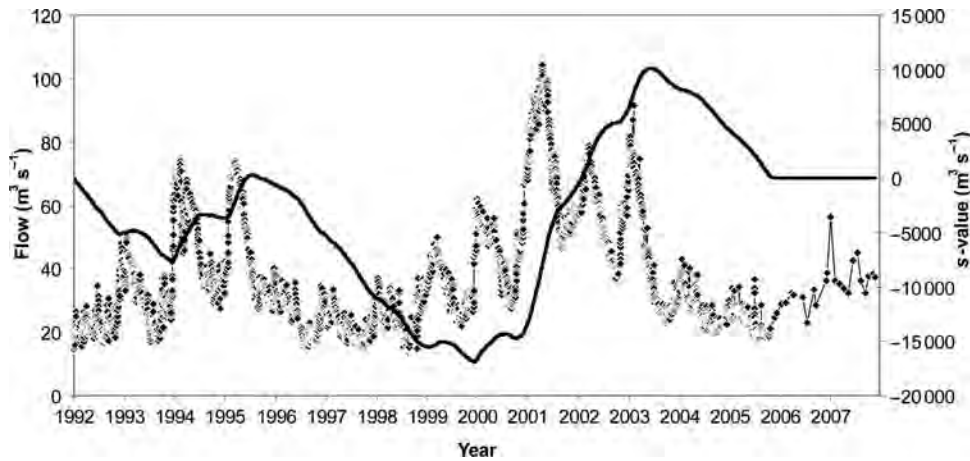
Figure 8. Daily flow of the River Somme (m^3 s^{-1}) during the period 1992–2007 and the associated cumulative function (heavy black line). The right-axis values correspond to *s*-values in the same units as the parameters considered (Data: Artois–Picardie Water Agency).

have diminished. This hypothesis moderates the conclusions of Gieskes *et al.* (2007) about the dominance of nutrient inputs originating from the Atlantic compared over river-induced eutrophication on the *Phaeocystis* component, but it shows the difficulty in proving a direct link between *P. globosa* abundance shifts and changes in its immediate environment (hydrodynamics, chemistry, accompanying species). Such an assumption could be checked through the use of physico-biogeochemical coupled models.

What needs to be looked at too is the fact that there seems to have been a regime shift just before the implementation of the SRN monitoring programme, the observed changes in the 1990s being a consequence of that shift. Indeed, several authors (e.g. Edwards *et al.*, 2006) outlined major regime shifts in the late 1970s, 1980s, and 1990s in the northeastern Atlantic and North Sea, with direct or indirect consequences on the major functional groups of marine organisms they studied (phytoplankton, zooplankton, benthos, and fish).

Conclusions

In his review, Paerl (2006) concluded that management strategies and approaches for reducing eutrophication in coastal areas will most likely need to be both site- and ecosystem-specific. He stressed the importance of being able to detect and quantify events that could structure the ecosystem and that could reveal changes in its structure and function.

The SRN network, launched at the start of the 1990s, made it possible to answer some questions related to seasonal and interannual trends in the evolution and major shifts in physicochemical and biological parameters, in coastal and offshore waters of the French eastern English Channel and southern North Sea. The strategy is particularly well-suited to the framework of the current assessment of the quality of coastal and offshore waters (Water Framework Directive and OSPAR directives). The results here are therefore important in helping stakeholders and experts develop river-basin management plans in such ecosystems.

The current policies of watershed and littoral water-quality assessment seemed to succeed in reducing nutrient point sources (essentially phosphate), but the reduction in diffuse sources (of nitrogen) still remain to be solved to reduce the eutrophication

process, detected by the high N:P ratios increasing at the start of the sampling period. As a consequence, the ecosystems studied show some signs of eutrophication and some recent shifts in the phytoplankton community, with increasing prevalence of some harmful algal species. Regular and massive *P. globosa* blooms were recorded throughout the area studied, but the regional causes of this human-induced eutrophication need to be evaluated carefully with due regard to other factors (e.g. transboundary nitrogen input, atmospheric input, climate change) acting on a larger scale but impacting the local dynamics.

Considering the short duration of the life cycle in phytoplankton, a study based on a more-specific taxonomic approach to phytoplankton dynamics (e.g. at species level) would be bound to fail with monthly or at best bimonthly sampling frequency of the SRN monitoring programme. Moreover, in a system which is under megatidal influence, with cycles lasting from 15 d (springs/neaps) to several hours (high tide/low tide), the sampling strategy of the SRN does not seem sufficiently accurate to permit the detection of the high-frequency changes that likely fuel the ecosystem dynamics. High-frequency *in situ* automated measurement systems (e.g. the MAREL station, which includes both nutrient and fluorescence measurements; http://www.ifremer.fr/delbl/presentation/marel/marel.htm) have been implemented at the Boulogne-sur-Mer site since spring 2004, and new research programmes have started, to complement the SRN approach by carrying out high-frequency assessments of phytoplankton dynamics using alternative techniques such as flow cytometry (Guiselin, 2010). These high-frequency approaches will be particularly well adapted to a study of the phenology of phytoplankton dynamics, which is important for understanding ecosystem quality, structure, and function, its reactivity to changes in nutrient input, and the match or mismatch between trophic levels and functional groups. In this way, we should be able to contribute to the implementation of an ecosystem approach to achieving sustainable use of the goods and services of marine ecosystems.

Acknowledgements

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