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Climatic control of *Phaeocystis* spring bloom in the Eastern English Channel (1991-2000)

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Abstract : The spring abundance of the prymnesiophyceae *Phaeosystis* sp. has been investigated in the coastal waters of the Eastern English Channel for 10 years (1991-2000). The North Atlantic Oscillation winter index was significantly correlated with the *Phaeocystis* abundance in April-May. Similar relationships between the North Atlantic Oscillation (NAO) and phytoplankton have been found in a variety of aquatic systems, including lakes, fjords and coastal areas, suggesting a general link between climatic forcing and phytoplankton dynamics. In particular, the negative correlation observed between the NAO and *Phaeocystis*, and the positive correlation observed between the NAO and diatoms in the Eastern English Channel support the hypothesis of a differential competitivity between *Phaeocystis* and diatoms for light and nutrient *via* hydrodynamic control.

Key words : *climate variability, English Channel, phytoplankton succession, Phaeocystis, diatoms, interannual variability*

1. Introduction

Climatic forcing is increasingly recognized as an important factor causing interannual variability in organism abundances in both aquatic and terrestrial ecosystems (*e.g.* LINDAHL *et al.*, 1998 ; BELGRANO *et al.*, 1999 ; STRAILE, 2000). More specifically, climatic forcing on physico-chemical and biological processes in the oceans has been regarded as an important aspect when untangling the complex dynamics of marine ecosystems (DICKSON *et al.*, 1988). Because of the economic importance of North Atlantic fish stocks, there is a long history of research to understand the variability in fisheries and ecosystems in this region (MILLS, 1989), and a real need to relate large-scale ocean-atmosphere processes to biological processes (KERR, 1997).

The North Atlantic Oscillation (NAO) can be regarded as a large-scale climatic oscillation based on the difference of normalized sea level pressures between the Azores and Iceland. The changes in NAO are reflected in an increase/decrease in the speed and direction of the westerlies, resulting in a regulation of winter temperatures on either side of the North Atlantic (HURRELL, 1995). The NAO impact on pelagic ecosystems has recently been shown to extend from the Barents and Norwegian Seas (SKJOLDAL *et al.*, 1992 ; HELLE and PENNINGTON, 1999), to the Nova Scotia Shelf (HEAD *et al.*, 1999) and the Gulf of Maine (CONVERSI *et al.*, 2001), including the Eastern and North Atlantic (FROMENTIN and PLANQUE, 1996 ; REID and PLANQUE, 1999 ; DICKSON *et al.*, 2000), the North Sea (STEPHENS *et al.*, 1998) and the English Channel (IRIGOIEN *et al.* 2000).

In the English Channel, IRIGOIEN *et al.* (2000) found a positive correlation between diatoms abundance and the NAO, and suggested that the meteorological conditions caused by positive NAO values in the North East Atlantic could favour diatoms compared with other groups or species, such as flagellates or *Phaeocystis*. In the nutrient-enriched Eastern English Channel and the Southern Bight of the North Sea, intense spring blooms (reaching biomass higher than 20 mg Chl *a* m^{-3}) are

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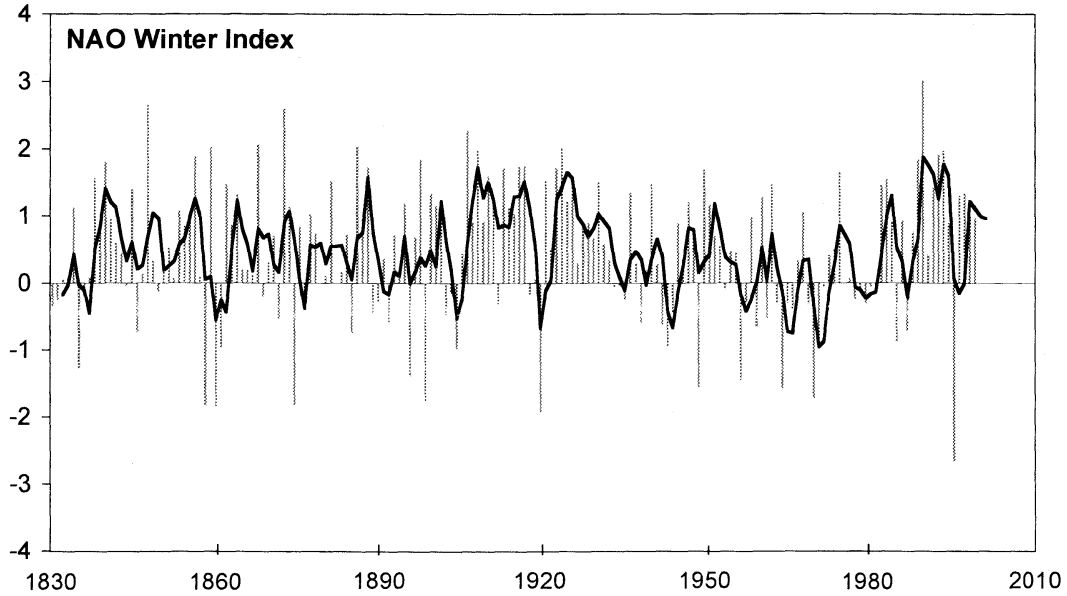

Fig. 1. The winter NAO index (HURRELL, 1995). The dark line is a three-year running mean of the yearly data.

recurrently composed of *Phaeocystis* and diatoms. Some hypotheses to explain the *Phaeocystis*/diatoms succession have been proposed, including differential competitivity for light and/or nutrients (MATRAI *et al.*, 1995 ; HEGARTY and VILLAREAL, 1998 ; PEPERZAK *et al.*, 1998 ; MOISAN and MITCHELL, 1999 ; MEYER *et al.*, 2000), but their determinism nevertheless remain unknown. While these hypotheses can be tested in the laboratory, large scale atmospheric forcing may also modify hydrodynamic regimes, and consequently abiotic and biotic factors related to encounter rates, growth and recruitment. However, no attention has been paid to the relation between *Phaeocystis*/diatoms abundance and atmospheric forcing.

In the present study a brief review of the main characteristics of the North Atlantic Oscillation and its effects on oceanic ecosystems will be presented. A 10-year time series of the abundance of the Prymnesiophyceae *Phaeocystis* in the English Channel will then be analysed jointly with the North Atlantic Oscillation data set, and finally a conceptual model for analysing the possible scenarios and the resulting processes which may control and regulate the observed fluctuations will be proposed.

2. The North Atlantic Oscillation and its ecological relevance

2.1 The North Atlantic Oscillation

The strongest and most well known mode of climate variability is the El Niño-Southern Oscillation (ENSO), a phenomenon originating in the tropical Pacific Ocean but impacting weather patterns and ecosystems around the world (MCPHADEN, 1999). Although the North Atlantic lacks an interannual mode of climate variability comparable in intensity to ENSO, it does exhibit an interdecadal mode, the North Atlantic Oscillation, as visible from Fig. 1 (NAO hereafter; HURRELL, 1995). Several indices have been developed to quantify the state of the NAO, but the most widely used index, Hurrell's NAO index (HURRELL, 1995), computes the pressure difference based on measurements from Lisbon, Portugal and Stykkisholmur, Iceland. In particular, NAO index values averaged from December to March have been used as a climatic index (HURRELL, 1995).

It can be thought that the recent increasing number of studies related to the NAO have been motivated by its trend toward a more positive phase over the past 30 years (Fig. 1).

The magnitude of this recent trend appears to be unprecedented in the observational record (HURRELL, 1995), and probably over the past several centuries as shown by paleoclimate data (STOCKTON and GLUECK, 1999). The most pronounced anomalies have occurred since the winter of 1989 (HURRELL, 1995; WALSH *et al.*, 1996; THOMPSON and WALLACE, 1998) when record positive values of an index of the NAO have been recorded. Moreover, the trend in the NAO accounts for several remarkable changes recently in the climate and weather over the middle and high latitudes of the Northern Hemisphere, as well as in marine and terrestrial ecosystems. Some of the main features of these changes are reviewed hereafter.

2.1.1 NAO and atmospheric circulation

The NAO has originally been described as a "seesaw" pattern with opposite temperature anomalies occurring on the eastern and western sides of the Atlantic (VAN LOON and RODGERS, 1978). This is accompanied by pronounced shifts in the storm tracks and related synoptic eddy activity which affect the transport and convergence of atmospheric moisture and can be directly tied to changes in regional precipitation. During positive NAO phases, a situation observed during much of the past two decades (Fig. 1), the increased pressure difference results in more and stronger storms crossing the Atlantic Ocean on a more northerly track, leading (i) to warmer, drier and milder conditions in central and southern Europe and in northern Canada and Greenland, and (ii) to colder, stormier and wetter-than normal conditions in northern Europe from Iceland through Scandinavia and in the eastern North America (HURRELL, 1995, 1996; THOMPSON and WALLACE, 1998). In particular, this led to the advance of some northern European glaciers (SIGGURDSON and JONSSON, 1995) and the retreat of Alpines glaciers (FRANK, 1997). In contrast, during 1996, characterised by a negative NAO winter value (see Fig. 1), conditions were much drier than in other years, leading to increased wintertime precipitation over Scandinavia, and cold temperatures and heavy snowfalls throughout southern Europe.

2.1.2 NAO and mesoscale oceanic circulation

The atmospheric shifts associated with the NAO cause changes in sea-ice cover in both the Labrador and Greenland Seas as well as over the Arctic (CHAPMAN and WALSH, 1993; CAVALIERI *et al.*, 1997), pronounced decreases in mean sea level pressure over the Arctic (WALSH *et al.*, 1996), and changes in the physical properties of Arctic sea water (SY *et al.*, 1997), changes in North Atlantic surface wave heights (KUSHNIR *et al.*, 1997). The NAO has also been demonstrated to control the intensity of convection processes in the Labrador and the Greenland-Iceland Seas, and in the related position of deepwater formation (DICKSON *et al.*, 1996) which in turn influence the strength and character of the Atlantic meridional overturning circulation (REID and PLANQUE, 1999).

2.2 Ecological effects of the NAO

2.2.1 Phytoplankton populations

While climate fluctuations over the North Atlantic should influence phytoplankton standing stocks, little attention has been paid to the relation between phytoplankton dynamics and atmospheric forcing. Some results even appear to be divergent, and exact driving mechanisms remain unclear.

Recent studies in lakes reported positive correlations between the NAO and the percentage of diatoms in the phytoplankton (WEYHENMEYER *et al.*, 1999), and between the NAO and total phytoplankton biomass (ADRIAN *et al.*, 1999; STRAILE, 2000). Similar relationships have been shown in fjords with both phytoplankton biomass and abundance of three species of toxic dinoflagellates (LINDHAL *et al.*, 1998; BELGRANO *et al.*, 1999), and in the English Channel with diatoms abundance (IRIGOIEN *et al.*, 2000). However, in the North Sea phytoplankton community was negatively and positively related to the NAO before 1980 (DICKSON *et al.*, 1988) and after 1980 (REID *et al.*, 1998), respectively. Even considering the weakness of the latter correlation (REID and PLANQUE, 1999), these contradictory association between North Sea phytoplankton and the NAO may be reconciled considering the extension of the coastal jet reported by REID and PLANQUE (1999). Prior to the mid-eighties,

increased spring wind speeds related to positive NAO index values may have been responsible for the phytoplankton fluctuations through increased vertical mixing that leads phytoplankton cells to spend a significant amount of time below the compensation depth, i.e. the depth at which a phytoplankter's photosynthetic rate equals its respiration rate. During the mid-eighties, the coastal jet extended farther up the shelf and brought warm water into the North Sea. The warm water causing increased vertical density gradients which reduced the effect of wind mixing, even though the winds remained strong during the late eighties and early nineties (see Fig. 1), the phytoplankton stocks were high. In 1988, phytoplankton standing stocks increased dramatically (REID and PLANQUE, 1999), suggesting that the switch from wind-controlled to advection-controlled blooms occurred in that year.

2.2.2 Zooplankton populations

In marine ecosystems, the zooplankton species that received, to our knowledge, the greatest amount of attention is the calanoid copepod *Calanus finmarchicus*, a species abundant throughout the North Atlantic, especially during spring and early summer (MARSHALL and ORR, 1955). *C. finmarchicus*, together with *C. helgolandicus*, were the first zooplankton species whose fluctuations in abundance were directly correlated with the NAO (FROMENTIN and PLANQUE, 1996). During positive NAO years, the abundance of *C. finmarchicus* in the North Sea decreases, while the abundance of most other zooplankton species, including *C. helgolandicus*, increases. The reverse situation is observed during negative NAO conditions. FROMENTIN and PLANQUE (1996) proposed that changes in temperature associated with positive and negative NAO conditions (warmer and colder, respectively) control species shifts. Thus, *C. finmarchicus* and *C. helgolandicus*, typically found in colder and warmer waters, flourish during negative and positive NAO years, respectively. Alternatively, STEPHENS *et al.* (1998) suggested that increased flow from the north and west during negative NAO years advects large numbers of *C. finmarchicus* to the shelf region from their principle deep water overwintering habitat. Considering the effect of the NAO on the circulation patterns observed in the North Atlantic as described above, let us finally note here that the two previous hypotheses can be related by considering that temperature changes in the North Sea are determined by water mass movements: increased flow from the Norwegian Sea during negative NAO conditions would cool the North Sea and bring *C. finmarchicus* onto the shelf while displacing *C. helgolandicus* to the south.

The abundance of *C. finmarchicus* is also indirectly related to the NAO via circulation patterns in (i) the Barents Sea, where its abundance is driven by the warm Atlantic water flowing from the Norwegian Sea (HELL and PENNINGTON, 1999), and (ii) in the Gulf of Maine where a circulation-recruitment mechanism has been suggested (HEAD *et al.*, 1999; CONVERSI *et al.*, 2001).

3. The North Atlantic Oscillation and English Channel *Phaeocystis* abundance

3.1 Study area

The study area was located along the French coast of the Eastern English Channel (Fig. 2). The Eastern English Channel is characterised by its megatidal regime (the tidal range is one of the largest in the world, ranging from 3 to 9

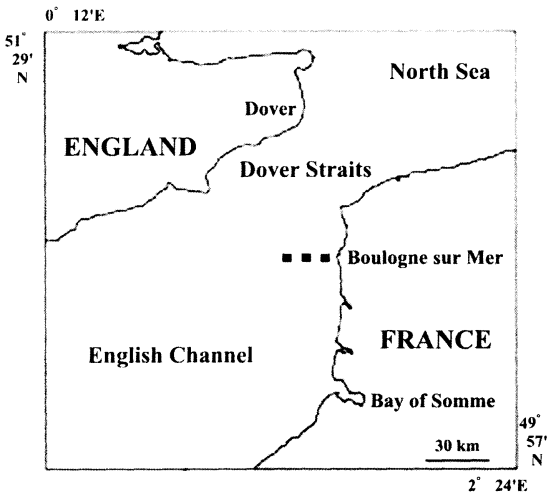

Fig. 2. Location of the sampling stations in the Eastern English Channel.

meters), and tides present a residual circulation parallel to the coast, with nearshore waters drifting from the English Channel to the North Sea. The freshwater run-off, distributed from the Bay of Seine to Cape Griz-Nez, generates a coastal water mass separated from the open sea by a tidally controlled frontal area (BRYLINSKI and LAGADEUC, 1990). This coastal flow ("fleuve côtier"; BRYLINSKI *et al.*, 1991) is characterised by its freshness, turbidity, phytoplankton and zooplankton (BRYLINSKI *et al.*, 1984; BRYLINSNKI and LAGADEUC, 1990) richness. Moreover, the dissipation of tidal energy is basically regarded to be responsible for the vertical homogenisation of inshore and offshore water masses (50 m maximum depth).

3.2 Data collection and analysis

Three stations, located from inshore to offshore waters of the Eastern English Channel (Fig. 2), were sampled fortnightly between January 1991 and December 2000 in the framework of a water quality survey conducted by the Centre IFREMER of Boulogne sur Mer (France). Water samples (500 ml) were taken using a bucket in subsurface water and preserved with formaldehyde. Subsamples (10 ml) were settled for 3 hours and counted with an inverted microscope. The results presented here correspond to the abundance of the Prymnesiophyceae *Phaeocystis* sp. in these samples. In the present paper, we only considered the spring bloom, which occurred during April-May (GENTILHOMME and LIZON, 1998). We then considered the abundance of *Phaeocystis* averaged over the three stations during April-May in further analysis. However, some samples were not collected because of bad weather conditions. In particular, no samples were collected during the spring 1997, and during the spring 1996, only one sample was collected in the inshore waters and no samples were collected in intermediate and offshore waters. To ensure the relevance of our further analysis, we then did not consider the years 1996 and 1997 in the analysis. Yearly NAO winter index(December-March; HURRELL, 1995) were used as a climatic index. Pearson correlation analyses were then performed between the NAO winter index and transformed *Phaeocystis* abundance.

3.3 NAO and phytoplankton abundance

Figure 3 shows a significant negative correlation between *Phaeocystis* abundance and the winter NAO index ($r=0.78, p < 0.05$). The abundance of *Phaeocystis* is then higher during years characterised by a low, and virtually negative NAO values. One needs to be aware here that in the English Channel and in the Southern Bight of the North sea, *Phaeocystis* appears to be co-occurrent and/or in competition with diatoms (*e.g.* ROUSSEAU, 2000). Considering the hypothesis of a climatically driven competitivity between these two genera, the abundance of *Phaeocystis* and diatoms should be negatively and positively correlated with the NAO winter index. The diatoms abundance indeed appears to be positively correlated with the NAO winter index from 1993 to 1999 in the English Channel (IRIGOIEN *et al.*, 2000). The corresponding positive regression has been plotted together with the *Phaeocystis* / NAO regression for comparison (Fig. 3).

4. Discussion

Meteorological conditions caused by negative NAO values are lower wind stress and stronger light due to decreased cloud coverage (HURRELL, 1995; Fig. 4). Such conditions could then favour *Phaeocystis* compared with diatoms that needs stronger mixing and lower light intensity (MARGALEF, 1967, 1978). On the other hand, lower nutrient levels associated with lower rainfall and the subsequent decrease in river run-off (Fig. 4) should favour *Phaeocystis* to the detriment of other phytoplankton species, in particular diatoms (MARGALEF, 1967, 1978). More precisely, we will discuss in the following how nutrient competition and light competition hypotheses, combined with the results presented in the previous section can be suggested to provide a phenomenological explanation to the response of *Phaeocystis* sp. and diatoms to climatic forcing.

The negative phases of the NAO winter index leads to a decrease in the intensity of the westerlies. The wind forcing in the SW-NE direction is then weaker, leading to less nutrient

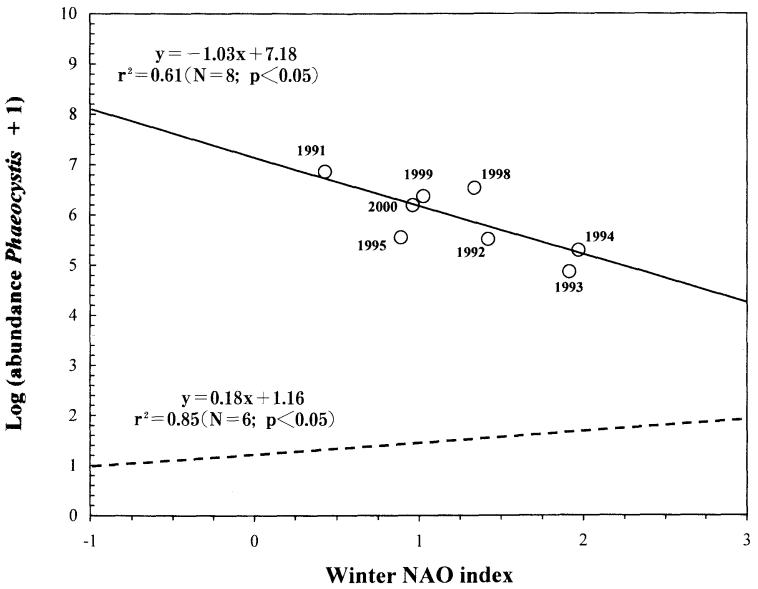

Fig. 3. Relation between the NAO winter index and the abundance of *Phaeocystis* sp. from 1991 to 2000. No data were collected in 1997, and the abundance resulting from the single sample collected in 1996 has not been considered in our analysis. The relation found by IRIGOIEN *et al.* (2000) between diatom abundance and the NAO winter index has been plotted for comparison (dashed line).

transport from the major fluvial inputs distributed along the French coast, especially from the Bay of Seine (Fig. 4), towards the Eastern English Channel. This effect is even more pronounced because of the decreased rainfall, and thus fluvial run-off, occurring during negative NAO phases. Nutrients, and in particular nitrates are then less available for phytoplankton growth, leading to a predominance of the genus *Phaeocystis*, more competitive for nitrates than diatoms (LANCELOT and BILLEN, 1985 : LANCELOT *et al.*, 1986). This functional scenario can also be applied to the Southern Bight of the North Sea, but with opposite consequences: weaker westerlies should lead to a greater extent of the flume of the Escaut estuary southward, to a greater nitrate availability and finally to predominance of diatoms in spring phytoplankton assemblages during the negative NAO years (Fig. 4). This hypothesis is supported by the positive correlation observed between salinity and spring *Phaeocystis* abundance in this area (ROUSSEAU, 2000), and suggests that the *Phaeocystis*/diatoms succession is mainly controlled by nutrient availability in the Southern Bight of the North Sea.

We argue that the colony form of *Phaeocystis* can also be regarded as an adaptation to lower turbulent conditions occurring during negative NAO phase. The impact of turbulence on nutrient flux toward a single free-living cell or a colony is dependent on its size relative to the viscous Kolmogorov length scale in the ocean, $l_k = (v^3/\varepsilon)^{0.25}$, where $v(10^{-2}\,cm^2.s^{-1})$ is the kinematic viscosity of sea water and $\varepsilon\,(cm^2.s^{-3})$ is the turbulent energy dissipation rate. Above this scale the flow is turbulent, while below it, viscosity dominates resulting in a laminar shear. This shear $S(s^{-1})$ is defined as $S = (\varepsilon/v)^{0.5}$ (KARP-BOSS *et al.*, 1996). The lower wind stress associated with low and negative NAO winter index leads to weaker dissipation rates ε, and larger viscous length scale l_k. The surrounding environment of small phytoplankton cells will then be more viscous than for larger cells. The shear is then smaller for smaller diatom cells (e.g. 5, 25 and 30 μm in diameter for *Thallassiosira, Rhizosolenia* and *Chaetoceros* cells) when compared with a *Phaeocystis* colony of several millimetres in diameter

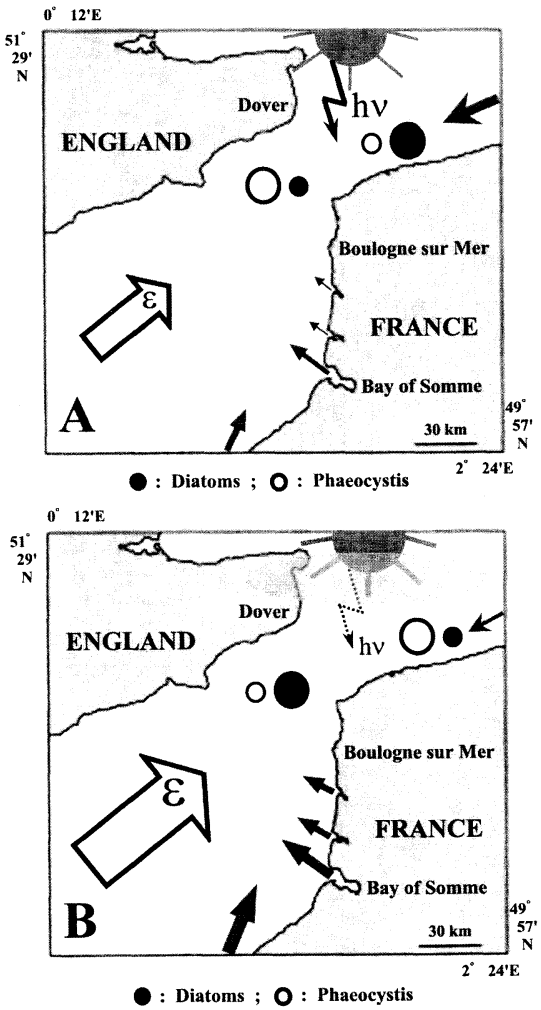

Fig. 4. Illustration of atmospheric conditions over the Eastern English Channel related to the NAO negative (A) and positive (B) phases, shown together with the dominant species in phytoplankton assemblages. During NAO negative phase (A), the weaker intensities of the westerlies (white arrow), leading to a weaker vertical mixing (ε), the decreased cloud coverage and decreased rainfall, and thus fluvial run-off (grey arrows) favour *Phaeocystis* sp. in the Eastern English Channel. During NAO positive phase (B), the stronger intensities of the westerlies, the increased cloud coverage and rainfall rather favour diatoms. Alternatively, in the Southern Bight of the North Sea, phytoplankton composition seems rather to be related to the nutrient availability controlled by the extent of the flume of the Escaut estuary, extending further south during negative than positive NAO phases.

(ROUSSEAU *et al.*, 1994). The subsequent nutrient flux towards diatom cells is then less efficient than towards the *Phaeocystis* cells within a colony (SEURONT, 2001). This difference in characteristic scales then provides the first phenomenological explanation for the competitive advantage of the colonial form of the genus *Phaeocystis* for nutrients when compared to diatoms, and under nutrient limitations.

Using a modelling approach, HUISMAN *et al.* (1999) showed that with high mixing rates (i.e. positive NAO phases), the species with the lowest critical light intensity (i.e. diatoms; see *e.g.* HEGARTY and VILLAREAL, 1998) should become dominant. On the contrary, with low mixing rates, species with low critical light intensity would be displaced by those able to obtain a better position in the light gradient. These theoretical results are fully congruent with the light control of cellular photosynthesis and exopolymeric synthesis by *Phaeocystis* colonies (LANCELOT and MATHOT, 1987). Moreover the buoyancy properties of *Phaeocystis* (SKRESLET, 1988), in particular those related to the colony form(LANCELOT and ROUSSEAU, 1994; LANCELOT, 1995), may be suggested as a secondary adaptation to light competition, leading *Phaeocystis* colonies to remain in surface layers and to benefit from more efficient light conditions for photosynthesis, contrary to heavier cells like diatoms(KIØRBOE, 1993). The model of HUISMAN *et al.* (1999) also predicts steep transitions in the population composition and no gradual changes. Unfortunately, similar conclusions cannot be drawn from our *Phaeocystis* data because of the weak number of data points available for the year 1996 which is the only one to be characterized by a negative NAO winter index (cf. Fig. 1). All the observations conducted here nevertheless converge toward the hypothesis of a yearly climatic control of the relative spring abundances of the genera *Phaeocystis* and diatoms via their specific competitivity for light.

5. Conclusions

This paper demonstrates the ability for climate variability to control phytoplankton succession in coastal waters of the Eastern English

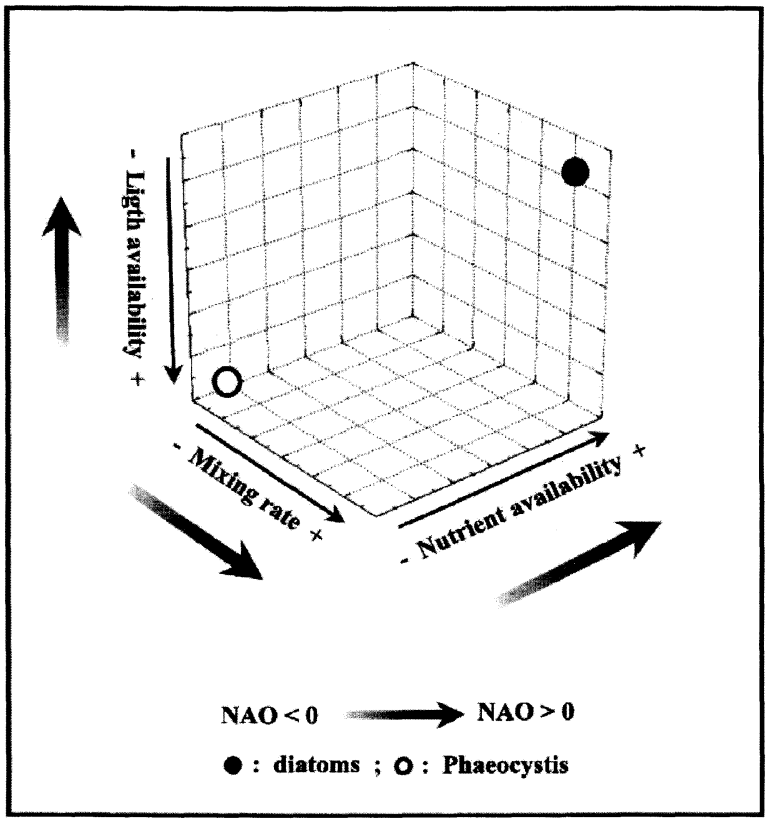

Fig. 5. Three-dimensional Intanglio which allows selection of species (*Phaeocystis* sp. or diatoms) in the Eastern English Channel, in a wide ecological space defined by both light and nutrient ability, and the intensity of mixing rates.

Channel *via* species specific adaptation to light and nutrient competition. In particular, taking into account the main meteorological conditions caused by the North Atlantic Oscillation, i.e. a lower wind stress, increased light due to decreased cloud coverage, and increased nutrient availability due to increased rainfall and subsequent fluvial run-off occurring during positive NAO phases, we propose a three-dimensional refined version of the Margalef's Mandala (MARGALEF, 1978 : MARGALEF *et al.*, 1979) and Reynolds Intaglio (REYNOLDS, 1987) for the control of *Phaeocystis*/diatoms succession in the Eastern English Channel (Fig. 5).

Finally, one needs to be aware that the growing awareness of the role of large-scale climatic forcing is not a matter of fact in marine ecology in particular, but rather seem to be the rule in ecological science in general. In particular, the 1042 references resulting from a survey of all papers reporting the terms 'climate', 'ENSO' and 'NAO' that appeared in the journals *Science* and *Nature* respectively from 1995 to 2001, and 1996 to 2001 stress the need to relate large-scale ocean-atmosphere processes to biological processes that clearly appears as a new challenge for oceanographers.

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