THE DIATOMS *Odontella sinensis*, *Coscinodiscus wailesii* and *Thalassiosira punctigera* IN THE EUROPEAN ATLANTIC: RECENT INTRODUCTIONS OR OVERLOOKED IN THE PAST?

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ABSTRACT

The diatoms *Odontella sinensis*, *Coscinodiscus wailesii* and *Thalassiosira punctigera* are the most common examples of non-indigenous phytoplankton species in the European Seas. We investigated their seasonal and inter-annual distributions at two fixed stations in the northeast English Channel (1998-2005). The climate conditions along our 8-y time series and those during the first historical outbreaks in Europe were reconstructed. *Odontella sinensis* was preferentially found in late summer and early autumn, especially after 2003. A change in the climate in 1903 may have favoured the development of *O. sinensis* that until then had gone unnoticed due to the low sample coverage. *Coscinodiscus wailesii* was preferentially found in winter and early spring, with a maximum in April 2001 (720 cells L^{-1}). This coincided with exceptionally high precipitation rates, river discharges and a cold winter (negative phase of the North Atlantic Oscillation). *Thalassiosira punctigera* was sporadically found between autumn and early spring, with a peak in mid-December 2005 after abnormal autumn weather. The blooms of *C. wailesii* and *T. punctigera* in 1977-79 coincided with the arrival of the 'Great Salinity Anomaly' into the English Channel, negative NAO phase and higher river discharges. In addition to an introduction from sub-arctic waters, these two diatom species may remain as residual populations under 'normal' hydro-climatic conditions, misidentified, overlooked in the past and favoured after atypical climate periods. The consideration for these diatoms being labelled as introduced or non-native species is questionable.

KEYWORDS: biological invasions, climate change bioindicators, invasive species, non-native diatom, North Atlantic Oscillation, weather variability

INTRODUCTION

The impacts of global climate change on earth's ecosystems are the subject of an increasing number of studies. Biological invasions are being recognized as an important element of global change, following the observation of increasingly spectacular developments of alien species in various regions of the world [1]. It has become obvious that human activities are responsible for massive movements of species, i.e. ballast waters, between the different oceans of the world [2]. The local plankton communities may be altered as well as their invasibility by exotic species from other regions [3, 4].

The climate variability may determinate the adaptation success of the introduced plankton species. The North Atlantic Oscillation (NAO) is responsible for much of the variability of weather in the North Atlantic region, affecting wind speed and wind direction changes, variations in temperature and moisture distribution and the intensity, number and track of storms. In years of high (positive) NAO winter index (December through March), the strengthened westerlies bring warmer, maritime air over northwest Europe causing a rise in temperature, mild winters, cool summers and frequent precipitation. In years of low (negative) NAO winter index, the effect of the westerlies is suppressed causing the temperature to be more extreme in summer and winter leading to heatwaves, deep freezes and reduced precipitation [5]. A link between the NAO and the distribution of phytoplankton [6-9] and other marine organisms have been described [10].

Numerous studies have documented the establishment of non-indigenous phytoplankton in the European waters (see references in [3]). Three centric diatoms, *Odontella sinensis* (Greville) Grunow, *Coscinodiscus wailesii* Gran et Angst and *Thalassiosira punctigera* (Castracane) Hasle are the most common examples in the literature. *Odontella sinensis* was described from material collected at Hong Kong Bay [11]. In Europe, it was first noted after proliferation in the North Sea in 1903, being since then a common member of the diatom assemblage [12, 13]. This is the first example of introduced phytoplankton species in the literature, presumablely carried by ballast waters, from the Red Sea or Indian Ocean [12].

Coscinodiscus wailesii and *Thalassiosira punctigera* have a much later start than *Odontella sinensis*. *Coscinodiscus wailesii* is a giant diatom, considered as a new species from the coasts of the British Columbia [14]. In winter 1977, a high phytoplankton bloom associated with extensive mucus provoked the clogging of fishing nets in the southern English Channel [15, 16]. The organism responsible for this phenomenon was identified for several years as the giant diatom *Coscinodiscus nobilis* Grunow [17, 18]. It was reported for many years in other regions of the European Atlantic [19-22] and identified by R. Simonsen as *C. wailesii* (cited in [19]).

In addition to *C. wailesii*, another diatom identified as *Thalassiosira angstii* (Gran) Makarova was cited as a newcomer off Plymouth in 1978 [23]. Kat reported the proliferation of this diatom since March 1981 along the Dutch coasts [24]. Rincé and Paulmier also cited its presence in the English Channel since 1978 [19], and Hasle in the Skagerrak since 1979 [25]. This diatom began to receive increased attention and Hasle proposed that *T. angstii* be identified as a synonym of *T. punctigera*, a species of problematic identification described under different names [25]. It was abundant in the English Channel in the years 1980-1981, but declined in later years [26]. *Odontella sinensis*, *C. wailesii* and *T. punctigera* are the most famous examples of non-indigenous phytoplankton species in the European Seas [3, 4].

The analysis of the phytoplankton seasonal and interannual variability would greatly aid in the detection of the arrival and the interpretation of future movements of the plankton species. The Strait of Dover, the maritime corridor between the English Channel and the North Sea, is a key area for the study of the distribution of plankton species in the European Atlantic. This region is under the influence of the Seine River, the main supplier of freshwater into the English Channel, which discharges contribute significantly to the nutrient load transported northward along the French coasts through the 'coastal flow'. The French national SOMLIT (Service d'Observation en Milieu LITtoral) monitoring program was established off Bolougne-sur-Mer (NE English Channel) in November 1997. We examined the evolution of *Odontella sinensis*, *Coscinodiscus wailesii* and *Thalassiosira punctifera* along an 8-y time series in order to establish their seasonal and interannual variability. In addition, we reconstructed the climate-environmental conditions when the first outbreaks of these species were reported in Europe. The combination of these data aims to elucidate between two hypothesis for the biogeographical origin of these species: 1) human-induced introduction (i.e., ballast waters, imported oysters), or 2) these species were already present as minor component of the phytoplankton, they were overlooked in the past, or they are now receiving attention after an anomalous set of climate conditions triggered the proliferations.

MATERIALS AND METHODS

Overall, 158 cruises were carried out on board the R/V *Sepia II* from November 1997 to December 2005 off Boulogne-sur-Mer (NE English Channel) (Fig. 1). Two fixed stations were sampled during the high tide. One station was located 2 km offshore (50°40.75'; 1°31.17' E; 21 m depth) and influenced by 'coastal flow' and the other station was 8 km offshore (50°40.75'N; 1°24.60'E, 50 m depth). The sampling frequency was planned to be biweekly, but cruises were sometimes cancelled or restricted to the close to shore station due to meteorological constraints. Sea-water samples were collected with a Niskin bottle at the surface and at one meter above the bottom. Lugol-fixed samples of 25 or 50 mL were settled in composite settling chambers. The entire chamber was scanned at 200× magnification with an IX71 inverted Olympus microscope and specimens were photographed at 400× magnification. The sample analysis of the 8-y time series was carried out with the same methodology and by the same observer.

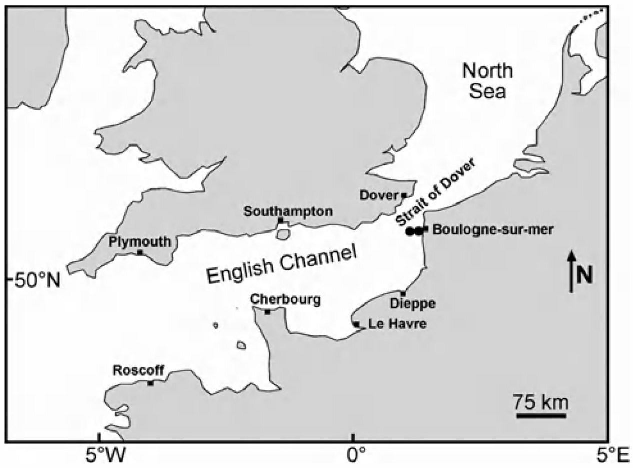

FIGURE 1 - Map of the English Channel. Sampling stations indicated by solid circles.

Continuous records of air temperature, precipitation, wind strength and direction (0-360°) were provided by the French Meteorological Agency (Météo-France Boulogne-sur-Mer) from a meteorological station located at Boulogne-sur-Mer (50°44'N, 1°36'E, altitude 73 m). These data are represented as average values per season. North Atlantic Oscillation winter index, hereafter abbreviated as -NAO_w-, was downloaded from the National Center for Atmospheric Research website (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). Daily river discharges of the Seine measured at Poses dam are obtained from the GIP Seine-Aval (http://seine-aval.crihan.fr/).

RESULTS

Weather conditions

In proximity to the Strait of Dover, the strong winds enhanced the northward current from the English Channel into the North Sea. The mean wind direction along the 8-y time series was 179° (southerly winds). This dominant wind direction is altered by westerlies (values closer to ~210°) with moist Atlantic air and the north - or south - easterlies (values closer to ~150°) from the continent with extreme temperatures. As a general trend, this 8-y time series study revealed two main periods: 1998-2000 was predominated by a moderate or high positive NAO_w, (i.e. mild winters, strong winds and high autumnal precipitation), a transition period in 2001 and by a neutral, NAO_w ~0, in 2002-2005 (i.e. reduction of wind strength and higher weather variability, extreme winter and summer temperatures) (Fig. 2).

1998-2000 NAO positive phase and 2001 transition period. The 1998-2000 period was characterized by mild winters, abundant precipitation, especially in autumn and stronger winds with an important westerly component (Fig. 2). The NAO_w in 2000 showed the highest positive value of the 8-y time series (2.80). The general trend for a high positive NAO_w are strengthened westerlies that bring warmer, maritime air over northwest Europe causing a rise in temperature. After scarce precipitation in winter, the spring of 2000 showed the highest rainfall along the 8-y time series (Fig. 2F). The autumn of 2000 resulted showed the highest mean wind strength (7.38 m s^{-1}) with the highest component of westerlies (199°) for that season along the 8-y time series (Fig. 2M,N,O,P). The blowing of the maritime wind in autumn 2000 was associated with the highest autumnal precipitation values as compared to any other year (Fig. 2N).

In contrast to the previous year, 2001 is illustrated by the lowest (negative) NAO_w (-1.89) since 1996 (-3.78). The lowest winter temperatures (4.91 °C), lowest wind strength and direction (158°) for the 1998-2005 period were recorded in 2001 (Fig. 2A,C,D). The highest precipitations were recorded in autumn 2000 and continued to the winter of 2001, with values higher than those of any other winters (Fig. 2B). These precipitation rates were associated with the northerly and easterly wind events. In March 2001, the discharge of the Seine River resulted in the highest peak water level (2280 m^3 s^{-1}) over the last six decades (Fig. 3). The lowest April mean temperatures for the 1998-2005 period were recorded in 2001 (8.22 °C). Along with these factors, the water column mixing and river runoff were expected to increase the nutrient stock for the spring diatom bloom in 2001.

2002-2005 neutral NAO phase. Higher autumnal rainfall was recorded throughout the 1998-2000 period and was associated with higher wind strength and westerlies. In contrast, the autumn seasons of the 2002-2005 period were drier and the wind strength was reduced about 30-40% with a lower contribution of westerlies (Fig. 2N-P). In the period 2002-2005, the values of NAO_w were neutral (index ~0). A moderate positive NAO_w (0.76) in 2002 constituted the only exception. It showed the strongest winter winds (7.76 m s^{-1}) along the 8-y time series, along with an important contribution of westerlies. The maritime air contributed to an increased temperature, resulting in the one of the mildest winters (6.7 °C) in 2002 (Fig. 2A-D).

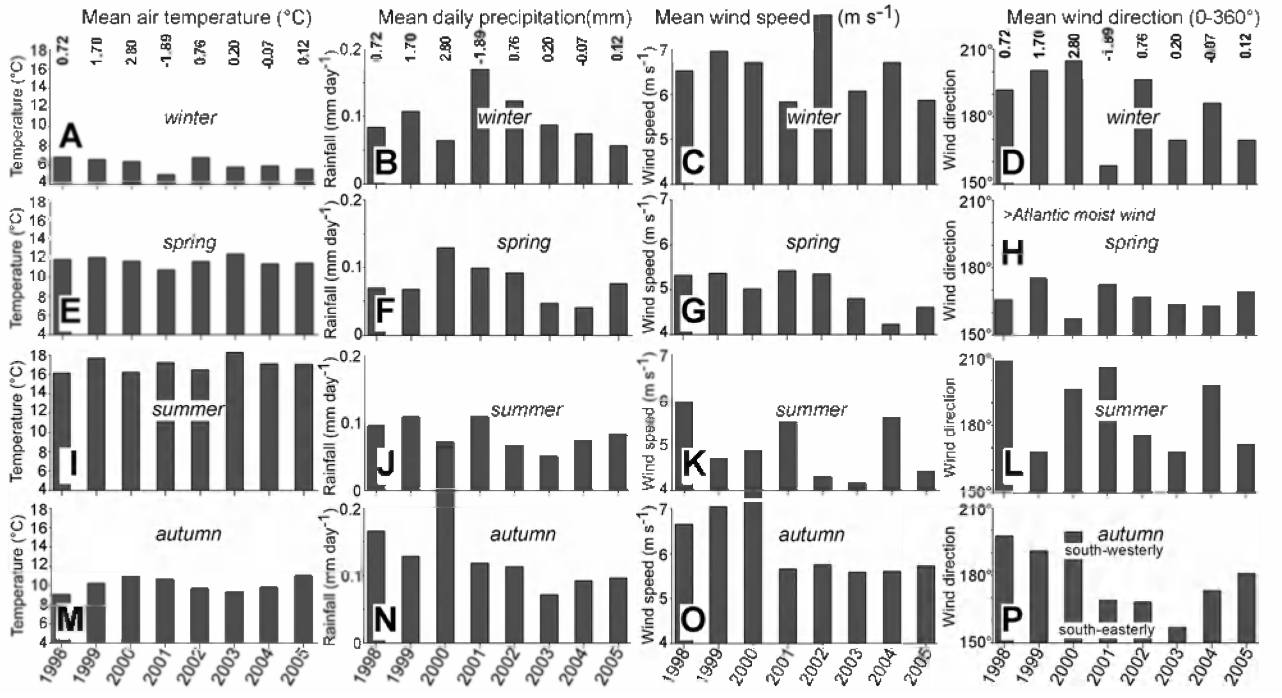

FIGURE 2 - **1998-2005 variations in monthly means of air temperature (°C) (A,E,I,M), daily precipitation (mm) (B,F,J,N), wind speed (m s^{-1}) (C,G,K,O) and wind direction expressed as degrees (0-360°) with respect to the north (D,H,L,P) in winter, spring, summer and autumn of the period 1998-2005 at Boulogne-sur-Mer. The NAO winter indices are indicated in the upper panels.**

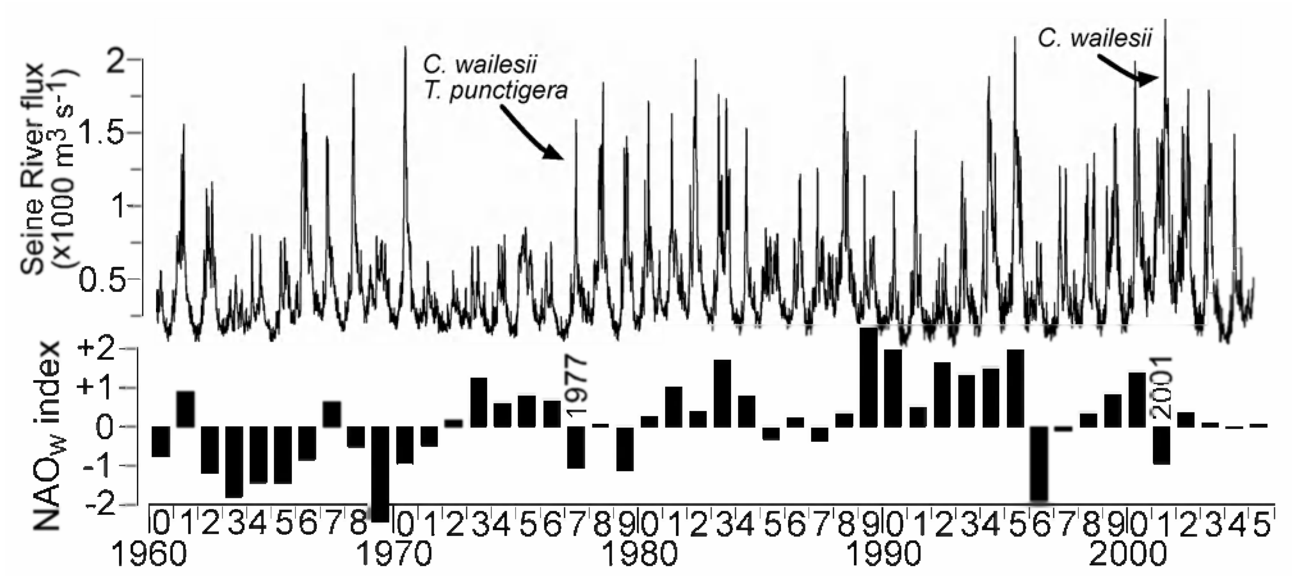

FIGURE 3 - Temporal evolution of freshwater discharges of the Seine River at Poses Dam. Source: http://seine-aval.crihan.fr/webGIPSA/; and the NAO winter index (December-March). Source: http://www.cgd.ucar.edu/cas/jhurrell/indices.html

The summer and autumn in 2002 and 2003 was represented by more stable weather conditions, lowered wind strength and decreased westerly winds (Fig. 2I-P). The summer of 2003 was the warmest recorded during the 8-y time series (Fig. 2I). In contrast, the autumn of 2003 demonstrated the second coldest temperatures (9.27 °C) and was the driest for the 1998-2005 period (Fig. 2M). The summer of 2004 incurred a higher wind strength and incidence of westerlies since 2001 (Fig. 2K,L). The highest mean autumn temperatures (10.97 °C), and the weakest mean winds for the 1998-2005 were recorded in 2005 (Fig. 2M-P). Under the stable weather, the Seine River had the lowest discharges in summer-autumn of 2003 and 2005 (Fig. 3).

Odontella sinensis

In the northeast English Channel the genus *Odontella* C.A. Agardh was represented by *O. aurita* (Lyngbye) C.A. Agardh, *O. mobiliensis* (J.W. Bailey) Grunow, *O. regia* (M. Schültze) R. Simonsen, *O. rhombus* (Ehrenberg) Kützing and *O. sinensis.* The last taxon is identified by its large size 100-250 µm (apical axis) and the flat or slightly concave valve face between processes (Fig. 4A-C). *Odontella sinensis* and *O. regia* may be confused with each other.

Although *O. sinensis* may be occasionally encountered throughout the entire year, it tended to reach higher abundances in early autumn. The species was not recorded in the years 2000 and 2002. Offshore (8 km), the abundance was lower than the more onshore station (2 km). Inshore, the abundance was higher on the surface, whereas in the offshore station the abundance tended to be slightly higher in deeper waters (50 m depth) (Fig. 5A-B). The interannual distribution of *O. sinensis* showed two peaks in October 2003 (3200 cells L^{-1}) and September 2004 (8000 cells L^{-1}). The warmest summer temperatures for the 1998-2005 period were recorded in 2003 (Fig. 2I). In contrast, the autumn of 2003 was the second coldest and the driest (Fig. 2M). These abnormal and contrasting weather phenomena seem to favour the peak of *O. sinensis* (Fig. 5A-B). In 2004, an unusual peak in abundance appeared in spring and early summer, with the greatest in September 2004. The lowest spring wind strength and precipitation for the 1998-2005 period were recorded in 2004 (Fig. 2F-G). The unusually calm conditions for spring 2004 seemed to favour the small peak of abundance. The calm spring was followed by a summer with the greatest wind strength since 2001, contributed by the westerlies (Fig. 2C-D). The anomalous meteorological conditions in the warmer seasons since 2003 may have favoured the proliferation of *a priori* warm-water species such as *O. sinensis* (Fig. 5A-B).

Coscinodiscus wailesii

This large, centric diatom (180-450 µm in valve diameter) had a rectangular outline in girdle view and the valves are flattened with a concentric depression. The valvar surface had hexagonal areolae with a sharp radial disposition and a hyaline central area (Fig. 4D-F). *Coscinodiscus wailesii* is occasionally recorded from late autumn to late spring, with peaks in winter and early spring. Inshore, the abundance was slightly higher on the surface. The highest abundance was recorded in April 2001 (720 cells L^{-1}). The abundance decreased since 2003, and was not detected in 2004 at all (Fig. 5C-D).

Thalassiosira punctigera

This diatom is smaller in size than the previously mentioned taxa (40-100 µm in diameter). The most distinctive characteristic is the ring of strutted processes (fultoportulae)

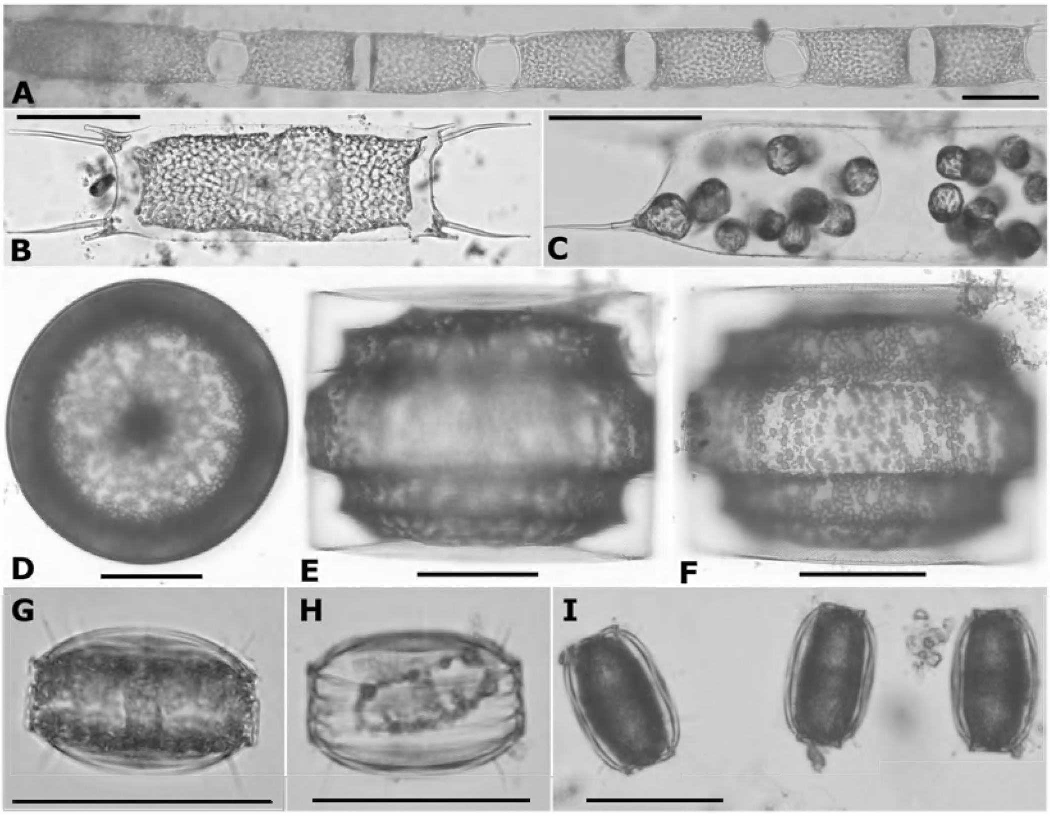

FIGURE 4 - Photomicrographs of *Odontella sinensis* (A-C), *Coscinodiscus wailesii* (D-F) and *Thalassiosira punctigera* (G-I). Scale bars = A-F: 100 µm, G-I, 50 µm.

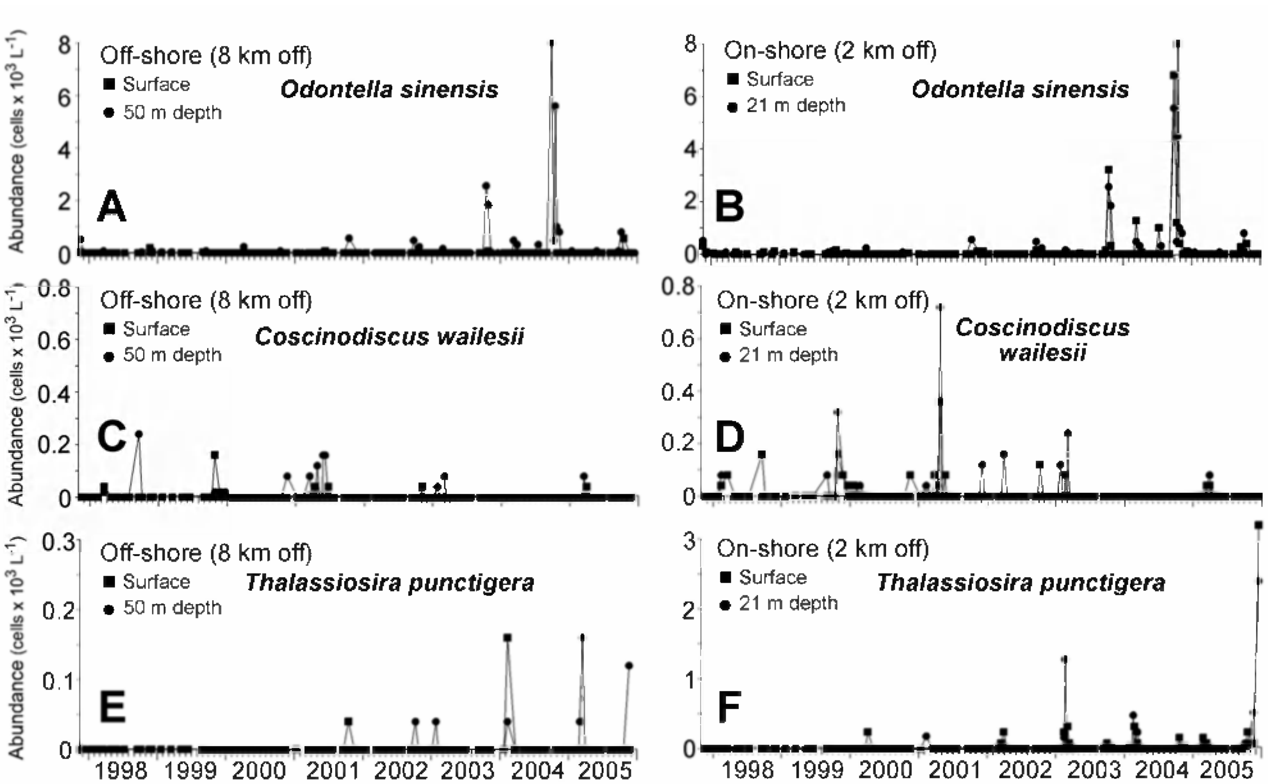

FIGURE 5 - Temporal distribution of the abundance (cells ×10^3 L^{-1}) of *Odontella sinensis* (A, B), *Coscinodiscus wailesii* (C, D) and *Thalassiosira punctigera* (E, F) in the NE English Channel (1998-2005). Left and right panels for offshore and onshore stations, respectively.

on the margin of the valve that has short external tubes and a convex valve surface. It tended to appear as single cells or short colonies connected by a thin thread (Fig. 4G-I). The abundance rarely exceeded 150 cells L^{-1} and it was even less in offshore waters. It is difficult to establish a trend on the distribution of *T. punctigera* because the records are dispersed and can be found throughout the entire year, except in the summer. The highest abundance (3200 cells L^{-1}) was recorded in mid-December 2005 (Fig. 5E-F). The autumn of 2005, especially October, was the warmest of the 8-y time series (Fig. 2M). For example, the mean daily air temperature was 18.4 °C on October 30th and decreased to 2.9 °C on November 25th. The anomalous conditions prolonged the warm summer conditions until November when a drastic decrease in temperature was associated with a peak of *T. punctigera*.

DISCUSSION

Odontella sinensis

This diatom was described in an early study on marine plankton from the warm coast of southern China in Hong Kong Bay [11]. The distribution of *O. sinensis* along the 8-y time series in the NE English Channel revealed higher abundances since 2003. The summers and autumns of the period 2001-2005 (negative or neutral NAO_w) showed lower wind strength when compared to the 1998-2000 period. According to the literature, the summer of 2003 incurred a heat wave in August and was the warmest during the past 500 years [27]. Calmer conditions and higher temperatures, especially since 2003, seem to favour the occurrence of *O. sinensis*. However, the thermal stratification (stabilization) did not favour the nutrient inputs required for the proliferation of large diatoms such as *O. sinensis*. In 2003, there was a drastic transition between an exceptionally warm summer and extremely cold autumn. In October 2003, the first autumnal storms may have enriched the still warm waters, favouring the short bloom of *O. sinensis* (Fig. 5A-B). The intense wind strength in the summer of 2004 may have been responsible of the largest abundance of *O. sinensis* in September. The summer conditions extended to late October in 2005 (Fig. 2N). Under these unusually stable conditions in autumn, the development of *O. sinensis* was delayed until the beginning of November, which was later than usual and resulted in a smaller abundance (800 cells L^{-1}) in comparison to previous years (Fig. 5B).

Odontella sinensis was cited for the first time in Europe in 1903 [12]. However, Boalch [26, p. 232] reported "*Odontella sinensis* which came to Europe from the Far East in 1889 and spread throughout European water (Ostenfeld, 1908) and is now an important constituent of the winter and spring diatom flora". We are unable to find the source of the earlier citation from 1889, but in our sampling region, *O. sinensis* tended to appear in late summer and autumn. During the nineteenth century most of the world's taxonomic expertise and sampling effort was concentrated along the northern European coasts. Before 1903, especially in 1889, the sample coverage was low and it is not unusual that any diatom would be first cited in the North Sea before any other regions of the world [12].

Most of the large diatom species were first described from the European coasts. The pioneer study of Greville in 1866 reported numerous new species, such as *O. sinensis*, later found to be common in Europe [11]. However, the diatoms described from locations outside Europe should not be considered of exotic origin due to the scarce sampling coverage. For example, *Skeletonema costatum* (Greville) Cleve has been traditionally cited as one of the most common blooming diatoms in the estuarine and coastal European waters. As *O. sinensis*, *S. costatum* was first described in Hong Kong Bay, and it was not considered a non-indigenous species in Europe. *Odontella regia*, quite similar to *O. sinensis*, was described from the North Sea. In Chinese waters, *O. regia* is a common blooming species [28]. Due to the polymorphism of *O. sinensis* [29], *O. sinensis* may have been misidentified with *O. regia* before 1903. It is risky to consider *O. sinensis* as an introduced or non-indigenous species in European waters because presumably it went unnoticed before 1903. Recent studies have shown that the cosmopolitan diatom *Skeletonema costatum* sensu lato is composed of several morphologically and genetically distinct species [30]. Molecular methods have not been applied to investigate the genetic characteristics of the populations of *O. sinensis*, *C. wailesii* and *T. punctigera* in different world regions.

An environmental factor, such as a climate drift, may have triggered the proliferation of, until then, minor members of the phytoplankton assemblage. In 1903, after 3 years of negative NAO_w, the highest positive index (3.89) in 126 years (since the first index in 1864 and 1989) was recorded. It was in that year that a 12-y period of positive NAO phase began and *O. sinensis* became widely distributed throughout European waters. In our study, it was difficult to establish a relation between the distribution of *O. sinensis* and the positive or negative NAO_w due to a higher proliferation that coincided with neutral values, NAO_w ~0. The NAO_w is based on the atmospheric pressure recorded between December and March [5]. Consequently the NAO_w is not a good descriptor for the climate conditions of the summer and early autumn periods when diatoms, such as *O. sinensis*, proliferated. The NAO_w would be more useful for the phytoplankton that proliferated in winter and early spring (i.e. *C. wailesii*). Along our 8-y time series, *O. sinensis* proliferated in warm periods, especially after mixing events (nutrient inputs). This scenario may be similar to a harbour in a tropical region with warm waters and high nutrient inputs (type locality of *O. sinensis*). The climate conditions before 1903 may have been unfavourable for *O. sinensis*, being undetected due to the scarce sample coverage or misidentified with *O. regia*. The exotic origin of the early description of *O. sinensis* should not provoke the thought that it was a non-indigenous species.

Coscinodiscus wailesii

Coscinodiscus wailesii is a world-wide distributed species, known from all the ocean regions. The populations in the subarctic waters [31] are connected with the boreal waters of the Pacific and Atlantic Oceans. It is a common blooming species at both sides of the temperate-boreal North Pacific [32, 33] and the tropical Pacific [34-36] and cited at both sides of the temperate South Pacific [37, 38]. It is found mutually on either side of the South Atlantic [39, 40]. In the North Atlantic, it is cited from the Caribbean Sea [41] and the North American Atlantic coasts [42-44], with a massive bloom reported off Florida [45]. The blooms of *C. wailesii* seem to be more frequent in cold coastal waters with frequent freshwater inputs [33, 46]. The world-wide distribution of *C. wailesii* is contrary to the theory that it is a non-indigenous species in any location.

According to the literature, *C. wailesii* was first recorded in Europe in 1977. The records of large *Coscinodiscus* species in Europe are usually assigned to the species *C. asteromphalus* Ehrenberg, *C. centralis* Ehrenberg, and *C. concinnus* W. Smith, which are morphologically similar and may cause identification problems [20]. Studies based on clonal cultures have reported a high variability in the valve morphology of *C. concinnus*, which also include other forms comparable to *C. granii* Gough [47]. In addition, *C. wailesii* demonstrated a high intraspecific variability during clonal culturing methods [48]. Most of the giant *Coscinodiscus* species, easily collectable by net sampling in coastal-estuarine waters, were described in the earlier diatom studies along the nineteenth century. However, *C. wailesii* was described relatively late, in 1931, along the shores of British Columbia [14]. The original description, published in a local journal of a Marine Station from the Pacific coast may have gone unnoticed by European researchers. Unless since 1972, the Helgoland phytoplankton time-series, German North Sea, reported a large *Coscinodiscus* identified as *C. wailesii*. Wiltshire and Dürselen [49] reported "For this species, data in the electronic database were changed later - but not from all size classes. Examples: March 1972 *Coscinodiscus* sp. size class 400 µm was changed to *C. wailesii* later; May 1987 *Coscinodiscus* sp. size class 270 µm was changed to *C. wailesii* later".

Coscinodiscus nobilis renamed as *C. wailesii?* The responsible agent for the large blooms of phytoplankton in the winter of 1977 in the English Channel was identified as *C. nobilis* for several years [17, 18]. In later years, R. Simonsen (cited in [19]) stated that the responsible diatom for the plankton bloom in 1977 was *C. wailesii* instead of *C. nobilis*. The latter was described from the brackish waters of the Caspian Sea [50] and has been cited from the arctic [51], boreal (Okhotsk, Japan, China Seas) and tropical waters (Indonesia, Madagascar, Gulf of Guinea) (see references in [52]). Cleve-Euler considered it as a form of *C. concinnus* (=*C. concinnus* f. *nobilis* (Grunow) Cleve-Euler) [53]. *Coscinodiscus wailesii* and *C. nobilis* are similar in shape, size, the lack of a central rosette and the number of areolae in 10 µm. The valve is flat in *C. wailesii* and flat or slightly convex in *C. nobilis* [34, 54]. Baars [54] from a culture of *C. concinnus* observed two morphotypes, the normal voluminous form and a flatter form with a few intercalary bands. Baars observed that the absence or presence of a hyaline area and intercalary bands are not diagnostic criteria for the species separation [54].

Since the 1960s, *C. nobilis* and *C. concinnus* have been cited as separated species in the estuaries of Brittany, English Channel [55]. The studies on the morphology of *C. wailesii* over the last three decades have been numerous, revealing a high intraclonal morphological variability [48], whereas no study of *C. nobilis* has been published. Before the 1980s, the records of *C. nobilis* were numerous with the latest being completed in 1968 and 1971 [52, 56]. After the blooms in late 1970s, the citations of *C. wailesii* have been numerous, whereas *C. nobilis* has disappeared from the literature. *Coscinodiscus wailesii* is a common blooming species around Japan and China [32, 35, 46]. However before 1931, *C. nobilis* (also described as *C. cylindricus* Mangin) was the giant diatom found in these regions [57-59]. A comparative morphological study of both taxa is necessary to discard the hypothesis that *C. wailesii* is a synonym of *C. nobilis*. A study from material collected in the type locality of *C. nobilis* could solve these doubts. However, the current environmental conditions of the Caspian Sea are far from those in the nineteenth century [50].

Blooms in 1977-1983: Coscinodiscus wailesii or *C. nobilis* began to receive attention after the intense blooms in the winter of 1977. A set of climate-environmental factors triggered the population of *C. wailesii* as a true newcomer species and/or expanded the local populations of *C. nobilis* from the estuaries of Brittany into the English Channel. Cold, eutrophic waters with high freshwater runoffs characterize the type localities of both species, the coasts of the British Columbia and the Caspian Sea. Both *C. wailesii* and *C. nobilis*, are giant, non-buoyant, diatoms requiring high nutrient inputs (silicate) and water column mixing to proliferate.

In 1968, an incursion of fresh, cold polar waters, 'Great Salinity Anomaly', via the Denmark Strait propagated into the North Atlantic and arrived at the English Channel in 1977, the North Sea in 1978, apparently returned to the Icelandic region in 1982 [60]. After a positive NAO phase occurred from 1972, negative NAO phase was recorded in 1977 (-2.14) and 1979 (-2.25). The winter discharges of the Seine River were unusually low in the 1971-1976 period, whereas in the period 1977-1983 was recorded very high winter discharges (Fig. 3). The exceptional climate conditions in the period 1977-1979 favoured the *C. wailesii* blooms.

Blooms in 2001: The highest abundance in this study (720 cells L^{-1}) was recorded in April 2001. This observation coincided with a bloom associated with mucus production in the northern Bay of Biscay [61]. In 2001, a very low (negative) value of the NAO_w (-1.89) occurred. In March 2001, the highest peak (2280 m^3 s^{-1}) of freshwater discharges from the Seine River over the past six decades occurred (Fig. 3). The transition between a high positive NAO_w in 2000 (high autumnal precipitation) and a negative NAO_w in 2001 (the coldest and rainiest winter, high mixing) favoured the highest abundance of *C. wailesii* during the early spring of 2001.

Rincé and Paulmier [19] suggested the introduction of *C. wailesii* by ballast water transport or through the importation of Japanese oysters. In contrast, two hypotheses for the biogeographical origin of the new blooming species in 1977 are proposed: 1) *Coscinodiscus wailesii*, known from polar waters and the Atlantic coasts of North America [42], was transported by currents into the European Atlantic, where the bloom was favoured by the 'Great Salinity Anomaly', cold temperatures and freshwater inputs from 1977-1979; or 2) the local populations, previously misidentified with congeneric species, such as *C. concinnus* or *C. nobilis*, bloomed and expanded under the exceptional favourable conditions in 1977-1979.

Thalassiosira punctigera

Thalassiosira punctigera is a medium-size diatom (~50 µm in diameter), inefficiently retained by net sampling where its delicate processes are easily damaged, thus making identification difficult during routine analysis. According to Hasle [25], *T. punctigera* is an extremely variable species with regard to size and valve structure and may be confused with other species. This taxon, initially described as *Ethmodiscus punctiger* Castracane, has been further described as other species such as *Coscinodiscus verecundus* Mann, *Coscinodiscus angstii* Gran in Gran and Angst (= *Thalassiosira angstii* (Gran) Makarova) and *Thalassiosira japonica* Kiselev. *Thalassiosira licea* Fryxell and *T. lundiana* Fryxell are closely related species (see references in [25]). Hasle entitled her article "a widely distributed marine planktonic diatom" that discussed the cosmopolitan character of *T. punctigera* [25].

The proliferation of *C. wailesii* after the extreme conditions seen in 1977-1979 increased the interest in the new diatoms. Kat [24] revealed that *T. punctigera* (as *T. angstii*) was favoured by the freshwater inputs. *Coscinodiscus wailesii* and *T. angstii* were described from the same study and region [14]. Consequently both taxa may be favoured by similar climatic conditions. After the dry 1971-1976 period, the high precipitation during 1977-1983 favoured the development of *T. punctigera*. In the present study, the highest abundance of *T. punctifera* was recorded after a drastic decrease in temperature during the abnormal autumn in 2005. Minor components of the phytoplankton assemblage may have gone unnoticed for long periods due to the low abundance and/or difficult identification. During the abnormal hydro-climatic conditions, i.e. 1977-1979 or late 2005, the usual diatom assemblage may possibly have been altered, while rare species, such as *T. punctifera*, were allowed to proliferate. The non-indigenous character of *T. punctigera* was highly questionable.

CONCLUSIONS

The consideration of introduced species implies that: 1) it colonizes a new region where it was not previously present; (2) the extension of its range is linked, directly or indirectly, to human activity; (3) there is a geographical discontinuity between its native area and the new area (remote dispersal). This means that the marginal dispersal, occasional advances or withdrawals of a species at the frontiers of its native range linked to climatic episodes is not taken into consideration [2]. The diatoms, *O. sinensis*, *C. wailesii* and *T. punctigera*, did not achieve any of these conditions to be considered as non-native species in Europe. *Odontella sinensis* may have gone unnoticed due to the scarce sample coverage and the unfavourable conditions before 1903 or it was simply confused with *O. regia*. *Thalassiosira punctigera*, a minor component of the diatom assemblage, may have been easily confused with other congeneric species, which proliferated under the extreme climate conditions from 1977-1979. *Coscinodiscus wailesii*, known from the sub-arctic waters and the north-western Atlantic may have been transported by currents into the European Atlantic and bloomed due to the 'Great Salinity Anomaly' and the climate in 1977-1979. Conversely, the local populations, previously misidentified with other *Coscinodiscus* species, such as *C. concinnus* or *C. nobilis*, bloomed and expanded during the 1977-1979 period. In any case, this constituted a marginal dispersal linked to climatic episodes and it is not the introduction of exotic flora. It is questionable to consider these diatoms as introduced or non-native species in the European Seas. The lack of experts in taxonomy of phytoplankton in the monitoring programs makes it difficult to evaluate future changes in marine biodiversity.

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