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Case history and persistence of the non-indigenous diatom *Coscinodiscus wailesii* in the north-east Atlantic

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The introduction of non-indigenous marine plankton species can have a considerable ecological and economic effect on regional systems. Their presence, however, can go unnoticed until they reach nuisance status and as a consequence few case histories exist containing information on their initial appearance and their spatio–temporal patterns. Here we report on the occurrence of the non-indigenous diatom *Coscinodiscus wailesii* in 1977 in the English Channel, its subsequent geographical spread into European shelf seas, and its persistence as a significant member of the diatom community in the north-east Atlantic from 1977–1995.

INTRODUCTION

During the last few decades the introduction and geographical spread of non-indigenous marine species has become increasingly topical, as the appearance of such species can have important ecological and economic consequences (Reid, 1997). Introductions have special significance for phytoplankton as they may be associated with harmful algal blooms which may have adverse effects on other marine life, as well as endangering human health via shellfish poisoning and respiratory illness and as potential carriers of infectious diseases (Tester et al., 1991; Hallegraeff & Bolch, 1992; Epstein et al., 1995). Arising from growing concerns of the apparent increase in the occurrence of harmful algal blooms and species introductions, a number of international and national initiatives have recently been implemented to improve understanding and develop management and amelioration strategies.

The main vector for the dispersal of non-indigenous marine phytoplankton species via human activities is by the worldwide transportation of ships' ballast water and to a lesser extent aquacultural practices (Carlton & Geller, 1993). The idea that exotic species were introduced by ships' ballast water was first postulated by Ostenfeld (1908) who observed a large new Indo-Pacific diatom *Biddulphia* (now *Odontella*) *sinensis* Greville in the North Sea, previously known from the Red Sea and the South China Sea. Since then a number of invasive diatom, dinoflagellate and flagellate species have been identified in the North Sea (see Nehring, 1998; Elbrächter, 1999; and Reise et al., 1999 for comprehensive lists) and in the English Channel (Boalch, 1987a,b, 1994). Nehring (1998) and Boalch (1987b) noticed that while many new arrivals can be classified as temporary immigrants and initially may have an impact on the ecosystem, they often become rather localized (e.g. along frontal boundaries), disappear, or occupy an insignificant part of the community once balance has been restored. However, this is not the ecological fate for all invasive phytoplankton species, with some species becoming permanently established immigrants. Here we report on one such species, the non-indigenous diatom *Coscinodiscus wailesii* Gran & Angst, from its initial appearance, its subsequent geographical spread, and its recent persistence as a significant member of the diatom community in the North Sea.

Efforts to assess and monitor invasive marine species are at best fragmented, as they are typically only monitored or first noticed when the species reaches nuisance status (Hallegraeff, 1993) and as a consequence few case histories exist containing information of their spatial and temporal trends. Continuous Plankton Recorder (CPR) samples have been taken at a depth of 10 m in the North Atlantic Ocean from 1931 to 1939 and 1946 to the present. The CPR survey samples at monthly intervals over major regions of the North Atlantic Ocean and routinely identifies approximately 400 taxa of phytoplankton and zooplankton (Warner & Hays, 1994). Sampling by the CPR survey in the North Sea provides a comprehensive geographical network, allowing the systematic monitoring of changes in the plankton community in both space and time.

RESULTS AND DISCUSSION

Coscinodiscus wailesii is a very large centric diatom (175–500 μm in diameter) which was originally only known from essentially two regions, the first includes the Pacific coast of North America from southern California to British Columbia (Mahoney & Steimle, 1980) and the second includes areas of the Sea of China and Japanese coastal waters of the North Pacific Ocean (Kokubo, 1952; Nagai et al., 1995). The first occurrence of *C. wailesii* in the north-east Atlantic Ocean was reported by Boalch & Harbour (1977), who at the time identified it as *C. nobilis* Grunow. It was found in the Western Approaches of the English Channel from plankton samples taken just off Plymouth in January 1977. Plankton samples have been taken by the CPR survey at monthly intervals since the early 1950s in the Western Approaches and *C. wailesii* was first recorded in CPR samples (as *C. nobilis*) at 49°57′N

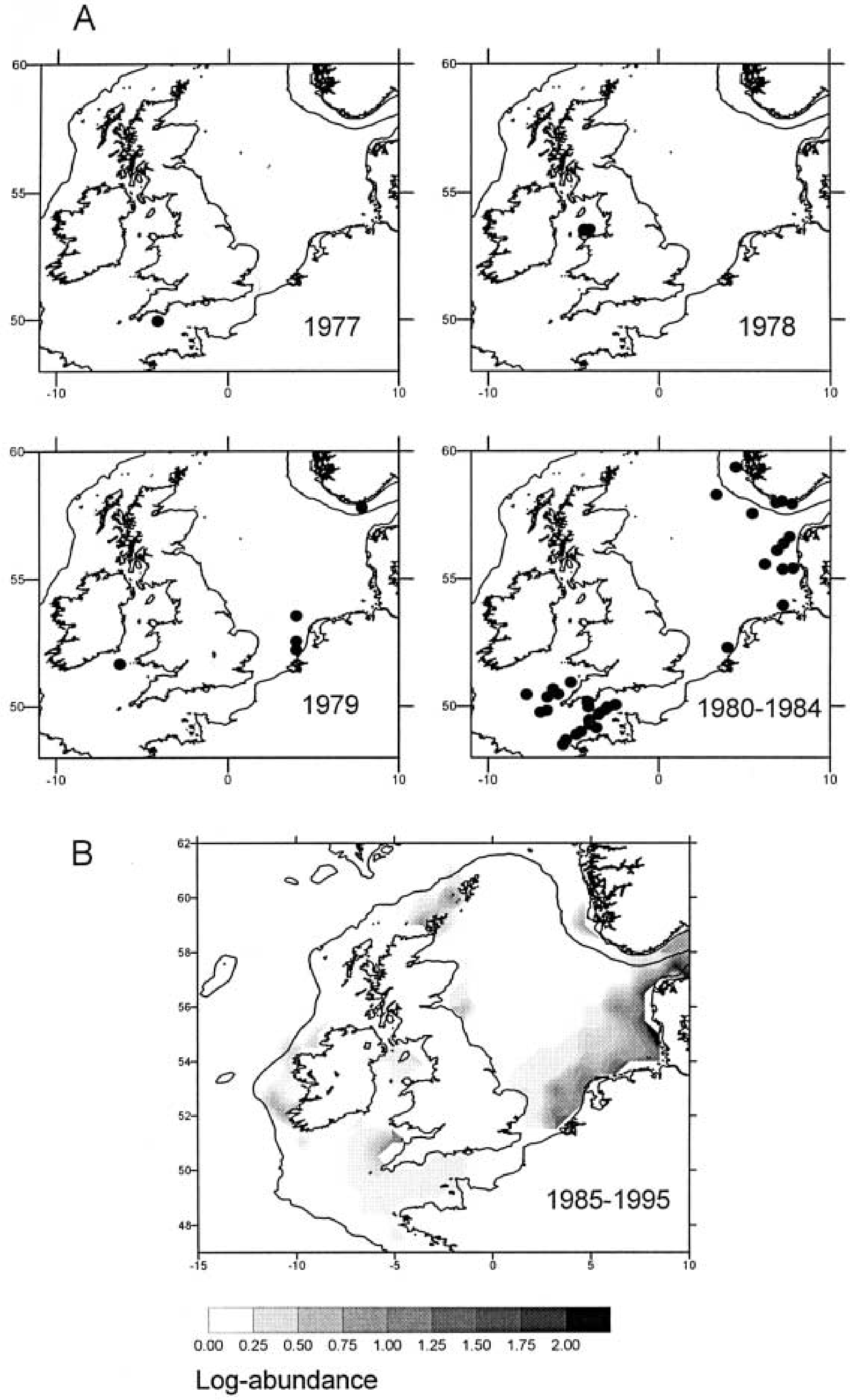

Figure 1. (A) Geographical distribution of *Coscinodiscus wailesii* in CPR samples in 1977, 1978, 1979 and from 1980 to 1984 in the north-east Atlantic; (B) geostatistical estimates of the mean log abundance of *C. wailesii* in CPR samples in the north-east Atlantic between 1985 and 1995. Density equates to log mean cell count per sample (~3m^3).

04°06′W (Figure 1A) in the spring of 1977 (Robinson et al., 1980). It is suspected that it was brought about by ballast water transport, although another potential vector may be via the importation of oysters from Japan and North America (Rince & Paulmier, 1986; Reise et al., 1999).

In 1978, *C. wailesii* first appeared in CPR samples in June and July in the northern Irish Sea, presumably carried north by current systems in the English Channel and Irish Sea. By 1979, *C. wailesii* had entered the North Sea and was found off the Dutch coast and at the entrance to the Skagerrak (Figure 1A), finally establishing itself within the Baltic Sea by 1983. The species was not found in CPR samples taken off Plymouth in 1978 or 1979. During the early 1980s the species continued to occur in these initial areas of establishment and also spread further east along the English Channel and further south along the Atlantic coast of France. In the North Sea, *C. wailesii* was frequently recorded in German and Danish coastal waters and in the waters off southern Norway. During 1985, *C. wailesii* was found in two new areas of the north-east Atlantic Ocean, off the south and west coasts of Ireland and in northern coastal waters of Scotland, principally around the Shetland and Orkney Islands. Outside the CPR survey's sampling network, *C. wailesii* has been recorded as far south as 46°N, along the Atlantic coast of France (Rince & Paulmier, 1986) and along the Norwegian coast to a northerly limit of 64°N (Karl Tangen, personal communication).

Successful invasions in aquatic systems may occur when native assemblages of organisms have been temporally disrupted by anomalous environmental conditions. This may be a determining factor in permanent establishment, particularly at the earliest stages of invasion. The North Sea shows considerable seasonal temporal disruption, with oceanic species sporadically entering the North Sea as a consequence of oceanic inflow. These species are simply extending their geographical range in response to changing environmental conditions and never establish permanent residence due to abiotic limitations once conditions return to normal. However, anomalous ocean climate conditions occur in the North Sea, which can persist for a number of years. One of the most anomalous periods in the North Sea over the last 40 years (both physically and biologically) occurred in the late 1970s. According to CPR survey records (data not shown), in the late 1970s phytoplankton diversity was low and seasonal patterns were anomalous (caused primarily by a delay in the spring bloom and a retarded seasonal growth period). For example, many early spring diatom species were absent and one of the most abundant diatoms (*Chaetoceros* spp.), normally present in March/April, was only recorded in small numbers in August during 1979. Temporal niches normally occupied by particular species were, therefore, abnormal during this period. Similarly, one of the most dominant dinoflagellates (*Ceratium macroceros*) experienced a population crash from an average recorded frequency of 40% on CPR samples in the 1960s to 0.4% during the late 1970s. It is presently open to question whether this exceptional period in the North Sea, caused primarily by unusual boreal conditions, left the ecosystem more susceptible to invasions (i.e. biotic resistance was low), or that the appearance of *Coscinodiscus wailesii* around this time was purely coincidental.

Since 1985, *C. wailesii* has become well-established in European continental shelf seas and in certain regions has become a significant member of the phytoplankton community, particularly during spring and autumn. Highest abundance is found along the southern North Sea coast and in the entrance to the Skagerrak, with sizeable populations now existing along the south-west coast of Norway, the western English Channel/Celtic Sea and the Atlantic coast of France, the northern Irish Sea, the west coast of Ireland, the Firth of Forth and in the coastal waters around the Orkney and Shetland Islands (Figure 1B). Its rapid establishment and success along the European continental coast and in the German Bight is particularly noteworthy, as the species can dominate the phytoplankton biomass over long periods in this area. Rick & Dürselen (1995) reported that during the period December 1988 to March 1989 the majority of phytoplankton carbon (up to 90%) in the German Bight could be attributed to this species. One likely reason for the success of *C. wailesii* and its ability to establish itself in new areas probably stems from its tolerance of wide temperature (from 0°C to >20°C), salinity (24–35 psu) and nutrient regimes (Dürselen & Rick, 1999).

Biogeographically the species appears to be most abundant in the neritic and well-mixed/transitional water masses of the north-east Atlantic Ocean. This is particularly apparent in the seasonally stratified northern North Sea, where the species is geographically restricted to transitional waters around the Orkney and Shetland Islands (see Pingree & Griffiths, 1978 for the position of frontal boundaries around the British Isles). The seasonal cycle of *C. wailesii* in the southern North Sea (Figure 2A) shows that the species dominates during the spring and autumn blooms. Highest abundance is found in April and again in September and October, with minima occurring during the summer months. The most sustained growth occurs during the autumn months. The long-term changes in *C. wailesii* in the southern North Sea, however, do not follow any discernible trend, with the population oscillating in abundance from one year to the next (Figure 2B). Although the species was first recorded by the CPR in the southern North Sea during 1979, it was not until 1984 that the species became established there and relatively high numbers were first recorded. Since its appearance in 1979, high numbers have been recorded in 1985, 1989 and 1990 and again in 1993 (from CPR data 1977–1995). It is not yet known why this species is particularly successful in one year and not in another and whether this is due to biological or physical constraints.

The appearance of non-indigenous species within a region can have both an important economic and environmental impact and this is certainly the case for *C. wailesii*. Although the species is non-toxic, when it first appeared in the north-east Atlantic it had a detrimental effect on fishing operations (Boalch & Harbour, 1977); this was also reported when the species was first recorded in the north-west Atlantic (Mahoney & Steimle, 1980). The species is capable of producing copious amounts of mucilage during bloom conditions to such an extent that this can clog fishing nets (Boalch, 1987). In Japanese coastal waters the species is considered particularly noxious as it causes serious damage to Nori (*Porphyra*) culture by removing nutrients such as inorganic nitrogen during winter and spring (Nagai et al., 1995). *Coscinodiscus wailesii* can reach such a high abundance it can dominate the phytoplankton biomass and therefore could have potential effects on the whole ecosystem by out-competing native species for resources/space, reducing biodiversity (NRC, 1995) and affecting exploitation rates of its primary production by native consumers. There is already evidence that *C. wailesii* can supersede indigenous phytoplankton species under certain conditions (Dürselen & Rick, 1999) and that two common indigenous herbivorous copepods of the southern North Sea find the species unpalatable (Roy et al., 1989).

In order to measure the ecological consequences of a non-indigenous species it is important to have base line information on the natural history of native species, and the community structure and biodiversity of the regional system under threat. Equally important is the ability to distinguish between community structural changes caused

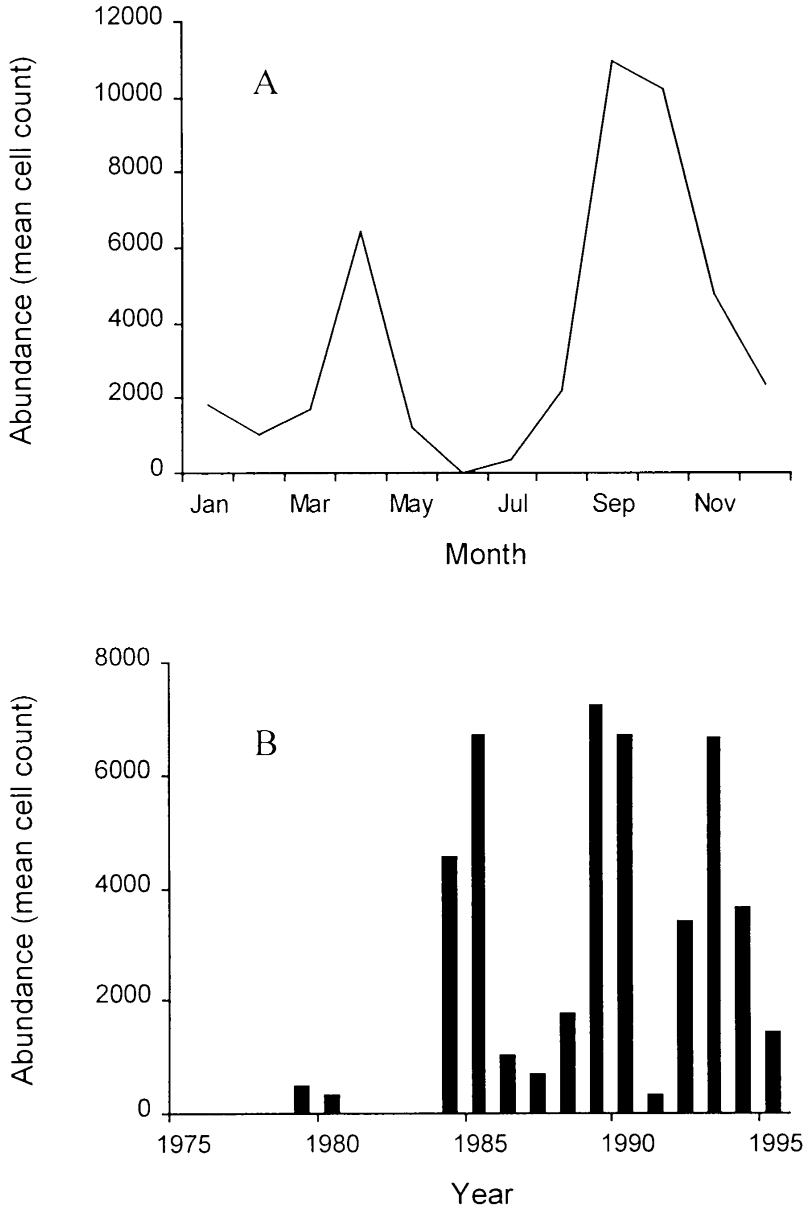

Figure 2. (A) Mean seasonal abundance of *Coscinodiscus wailesii* in CPR samples in the southern North Sea between 1985 and 1995. Density equates to mean cell count per sample ($\sim 3m^3$); (B) annual means of *C. wailesii* in CPR samples in the southern North Sea between 1975 and 1995. Density equates to mean cell count per sample ($\sim 3m^3$).

by invasive species and natural changes caused by climate variability. It has yet to be determined how much of the marked increase in phytoplankton biomass seen in the North Sea since 1985 (Reid et al., 1998) can be attributed to the increasing part that *C. wailesii* is now playing in the autumn and winter phytoplankton of the North Sea. This study is the first of its kind to show the spatial evolution of an invasive phytoplankton species over a decadal period. However, the consequences of shifting ecological roles in the North Sea in the long-term can only be determined by future observations. Whatever the source of phytoplankton introductions, measuring the patterns and rate of their spread is also essential in establishing the effectiveness of any management strategy put in place to limit invasions.

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