

# Non-indigenous phytoplankton species in the North Sea: supposed region of origin and possible transport vector

Stefan Nehring

*Federal Institute of Hydrology, Koblenz,  
Germany*

*Communicated by J. Lenz*

*Received: 7 March 1998*

*Accepted: 20 August 1998*

## Abstract

Over the past 100 years 16 non-indigenous phytoplankton species of the taxonomic groups Bacillariophyceae, Dinophyceae and Raphidophyceae have established persistent populations in the North Sea (excl. English Channel). A 17th non-indigenous species from the group Cyanophyceae was found in a brackish water basin on the North Sea coast. These species have either immigrated naturally, being transported by currents or were introduced by the activities of birds, in ballast water or in products of aquaculture. Thirteen of these new species have colonised the German Bight permanently (reflecting an increase in phytoplankton species numbers of about 1 %). The majority of these species are known mainly to frequent warmer waters.

## Kurzfassung

**Nicht-heimische Phytoplanktonarten in der Nordsee: Vermutete Herkunft und wahrscheinlicher Transportvektor**

Während der letzten 100 Jahre konnten in der Nordsee (exklusive Ärmelkanal) 16 nicht-heimische Phytoplanktonarten aus den taxonomischen Gruppen der Bacillariophyceae, Dinophyceae und Raphidophyceae dauerhafte Populationen etablieren. Eine 17. nicht-heimische Art aus der taxonomischen Gruppe der Cyanophyceae wurde in einem Brackwasserbecken an der Nordseeküste gefunden. Diese Arten sind entweder durch natürlichen Transport mit Meeresströmungen eingewandert oder wurden durch Transport mit Vögeln, in Ballastwasser oder in Aquakulturprodukte eingeschleppt. 13 dieser neuen Arten haben sich in der Deutschen Bucht dauerhaft angesiedelt (dies entspricht einer Zunahme in der Artenanzahl des Phytoplanktons von ca. 1%). Für die meisten dieser Arten ist bekannt, daß sie vorzugsweise in wärmeren Gewässern vorkommen.

## Introduction

A marine community is composed of indigenous species (endemic or native, whose length of existence in the community is generally unknown) and relatively recent invaders, species which did not formerly exist in the region (although, in rare instances, the species

may have existed in the region during an earlier geological period). The invasion of marine and estuarine systems by non-indigenous species is now a widely recognised phenomenon that continues to occur throughout the world at an increasing rate (*e.g.* Carlton 1989; Carlton and Geller 1993), but the ecological and evolutionary significance is poorly understood. Bioinvasions occur through two processes, range expansions and introductions. Range expansions consist of dispersal by natural mechanisms (*e.g.* currents, birds), whereas introductions consist of transportation, often across natural barriers by human activity (*e.g.* ballast water).

In some cases, these non-indigenous species have become numerically dominant in invaded communities and have significantly altered community function. However, in comparison to an extensive literature documenting the history and impact of invasions in freshwater and terrestrial habitats, relatively little information is available on marine invasions, especially for the phytoplankton of the North Sea. Finally, when species are identified as non-indigenous, information about their time of arrival, source, rate of spread, current distribution and effects on resident communities often remains poorly documented.

Over the past 100 years, a multitude of planktonic algae has emerged, that have not been previously observed in the North Sea, although few of them are genuinely new immigrants to these waters. The scope of this contribution is an intensive analysis of all available information about the establishment of non-indigenous phytoplankton species in the North Sea, their supposed region of origin and their possible transport vector. A review of this kind is necessary as a basis for discussions about the global spreading hypothesis (see Wyatt 1995) and can possibly help to clarify changes in plankton biocoenosis in relation to observed trends like eutrophication or climate change.

## Discussion

The first major inventories of North Sea phytoplankton were established about 100 years ago (*e.g.* Cleve 1887, 1900; Gran 1908; Paulsen 1908). Many more inventories followed and several monitoring programmes were set up (along the German North Sea coast since 1966, Drebes and Elbrächter 1976) so that today the North Sea can be considered to be one of the best-studied regions of the world for plankton.

During this time, a multitude of phytoplankton species, that had not previously been observed in the North Sea, has emerged. It is not always easy to say whether a "new" species has been overlooked in previous studies or whether it is a real newcomer. Today the scientific community is better informed and more aware of the signs and symptoms of plankton blooms. There has been an increased interest in plankton monitoring and more scientists are looking for "new" species.

### *Non-indigenous phytoplankton species: newcomer or overlooked?*

Whether morphologically conspicuous species have previously existed in the area can, in most cases, be deduced in the literature or by consulting experts. In the case of inconspicuous species like *Chrysochromulina*, *Pirsonia*, *Pseudo-nitzschia* or *Scrippsiella* it is quite

possible that most of them have gone previously unnoticed (e.g. Nehring 1994a; Hasle *et al.* 1996; Kühn *et al.* 1996; Vrieling *et al.* 1996). More light can be shed on this by re-examining historic sample collections which, however, may sometimes give unsatisfactory results. Old plankton records do not document the existence of certain species, collection (mesh size) and preservation techniques (strong fixatives) were often inadequate and the resulting species identification should be considered inconclusive.

Another problem arises from the difficulty there is in identifying a non-abundant newcomer species in large numbers of samples. The need for species-specific "probes" is clear – probes which can be used to label only those cells which are of interest so they can be detected visually, electronically, or chemically (Anderson 1995). Many different approaches have been developed (e.g. antibody probes, nucleic acid probes), but little effort has been put into studying non-toxic algal species until recently. The application of such modern techniques will help to reveal the cryptic presence of previously unrecognised invaders. It has a great potential for altering phytoplankton research but there is a great deal of work to be done to cover all scientific areas and to expand the availability of probes for all species of interest.

The possibility of analyzing pre-historic phytoplankton communities in inshore areas by the analysis of resistant resting forms in dated sediment depth cores has been little utilized. Since resting forms, like the cysts of dinoflagellates, can be fossilized, it becomes possible to track the development of dinoflagellate populations in response to factors such as climate change or anthropogenic impact. Thus, not only recent changes can be studied, but also those taking place over decades or even several thousands of years (Dale *et al.* 1993).

An important question in the identification of a newcomer species is whether it has really established a persistent population. The North Sea system is greatly influenced by variations in the North Atlantic current system and several species e.g. the Atlantic *Dinophysis odiosa* have occasionally been introduced by water currents (Elbrächter 1995). Relatively low water temperatures in winter, the absence of certain trace element, *etc.* prevent the development of permanent populations of such species. For other species (e.g. *Corymbellus aureus*, Gieskes and Kraay 1986; *Gonyaulax polyedra*, *Phaeopolykrikos hartmannii*, and *Protoperidinium compressum*, Nehring 1996, 1997; *Pleurosigma simonsenii* [syn. *Pleurosigma planctonicum*], Eno *et al.* 1997; *Thalassiosira tealata* [? syn. *Thalassiosira curviseriata*], Drebes pers. comm.), it is not yet clear what is their current status as immigrants in the North Sea area (excl. English Channel).

The following is a compilation of all the phytoplankton species which can, in the light of current knowledge, be considered genuine, established immigrants into the North Sea (incl. brackish water basins, excl. English Channel) having entered over the past 100 years.

### ***Recent phytoplankton introductions into the North Sea***

Altogether 16 newcomer species from the taxonomic groups Bacillariophyceae, Dinophyceae and Raphidophyceae have been identified which now constitute an integral part of the pelagic system in the North Sea (excl. English Channel). A 17th non-indigenous toxic species of Cyanophyceae has also been introduced into a brackish water basin on the North Sea coast (Figure 1).

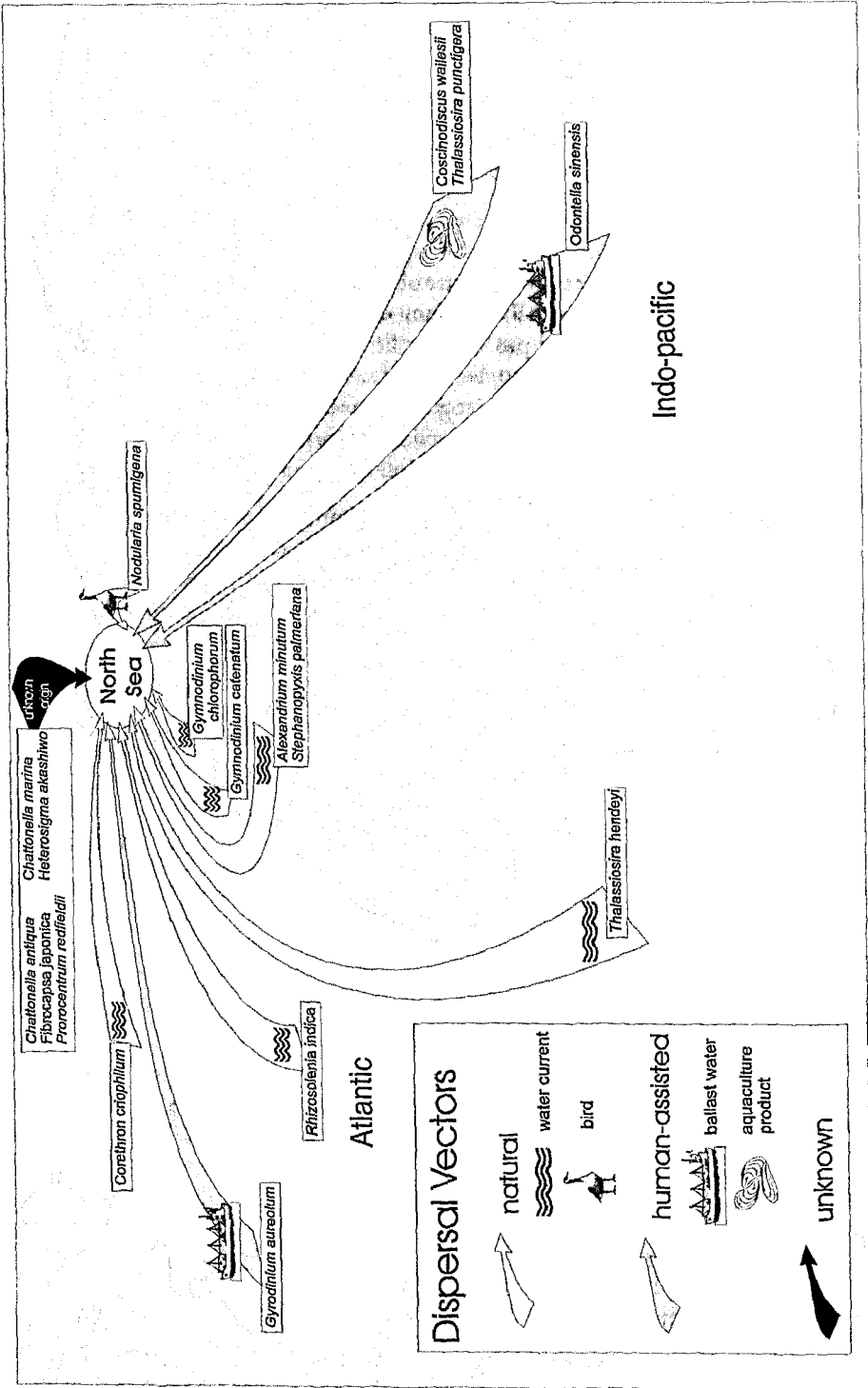


Figure 1: Global map summarising assumed introduction / immigration of non-indigenous phytoplankton species into the North Sea (excl. English Channel, incl. brackish water basins).

## Cyanophyceae

### *Nodularia spumigena* Mertens

In August 1990, a bloom of the toxic *N. spumigena* occurred in a brackish public bathing lake in the city of Wilhelmshaven on the German North Sea coast, causing the death of two dogs (Nehring 1993). Water quality in the lake had been monitored for several years by a town authority. Each year there was a characteristic low N/P ratio which favoured the development of cyanobacteria blooms (cf. Smith 1983). In Europe, the main distribution area of *N. spumigena* is the Baltic Sea. This species can develop spore-like dormant forms (akinetes), which retain their ability to germinate for many years, even under unfavourable environmental conditions (e.g. desiccation). Thus, it is very likely that *Nodularia* akinetes were transported from the Baltic Sea by birds (attached to feet or feathers or by internal transport in the digestive system, cf. e.g. Atkinson 1972, 1980) directly into the lake and may have triggered the algal bloom (Nehring 1993).

## Bacillariophyceae

### *Corethron criophilum* Castracane

This thin-walled, palely pigmented and thus easily overlooked species was identified in 1990 in the German Wadden Sea (Drebes 1991). The oceanic *C. criophilum* is an indicator species typical of Atlantic water and has occurred at irregular intervals for many years in the English Channel and in the central and northern North Sea. It is likely that mild winters have now enabled this species to colonise the North Sea (Drebes 1991).

### *Coscinodiscus wailesii* Gran and Angst

In 1977, *C. wailesii*, which had only previously been known in the Pacific and West Atlantic, was first observed in Europe in the English Channel. It was associated with an intensive production of mucus which clogged trawls and sometime caused damage to gear (Boalch and Harbour 1977). In the spring of 1984, mucus secreted by *C. wailesii* sunk the fixed nets of fishermen in the German Bight (Hagmeier 1992). This species, which is now present in North Sea plankton throughout the year (Hesse *et al.* 1996; Rick and Dürselen 1995), was probably introduced to northern Europe from the Indo-Pacific when French oyster farms began to cultivate the infection-resistant *Crassostrea gigas* (Rincé and Paulmier 1986).

### *Odontella (Biddulphia) sinensis* Grunow

In November 1903, the diatom *O. sinensis*, which had only previously been found in the Indo-Pacific and the China Sea, was discovered initially in the German Bight and then in the Skagerrak and the Kattegat (Ostenfeld 1908). In 1905 the species was found in Dutch waters (van Breemen 1906). It was assumed by Ostenfeld (1908) that *O. sinensis* was probably introduced into the North Sea with ballast water from the Indo-Pacific or neighbouring areas. Within a few years the species had spread over the entire North Sea.

*Rhizosolenia indica* H. Peragallo

This warm water species has occurred only very rarely during the last decades in the German Bight (Drebes 1974; Drebes and Elbrächter 1976). Since the end of 1989, *R. indica* has been found relatively frequently in the Dutch Wadden Sea. It is assumed that this species might be an addition to North Sea plankton, caused by the higher winter temperatures of recent years (Cadée and Hegemann 1991).

*Stephanopyxis palmeriana* Grunow

This species, which is indigenous to all oceans, prefers warmer waters, but the limits of its distribution are not sufficiently known because it is often mistaken for *S. turris* (Drebes 1991). In Europe, *S. palmeriana* is mainly found in the Mediterranean Sea, but when certain sea current patterns prevail, it may sporadically drift through the Strait of Gibraltar towards the British Isles (through the English Channel or around Scotland) and into the North Sea. Since 1990 this species has been found regularly in the German Wadden Sea (Drebes 1991). It is likely that mild winters have now enabled this species to colonise the North Sea (Drebes 1991).

*Thalassiosira hendeyi* Hasle and Fryxell

This diatom is considered a warm-water species and is well known in the coastal waters of the South Atlantic (Hasle and Fryxell 1977). In Europe, *T. hendeyi* was first recorded in 1978 near the mouth of the Dutch River Schelde (Rick 1990). It has been found relatively frequently in the plankton of the German Wadden Sea since 1995 (U. Tillmann pers. comm.). *T. hendeyi* possibly drifts with Atlantic water through the English Channel or around the British Isles via the Shetland Orkney Channel into the North Sea.

*Thalassiosira punctigera* Hasle

In 1978, *T. punctigera* was found for the first time in European waters in the English Channel (Kat 1982) and in 1979 its presence in the Skagerrak was proven (Hasle 1983). In 1981, it was found spreading along the Dutch coast into the German Bight (Kat 1982). Up until the 1980s, *T. punctigera* was only occasionally found in the eastern North Atlantic (Hasle 1983) whereas, it was frequent in the northern Pacific (Makarova 1970). Therefore it is assumed that this species was introduced from the Indo-Pacific along with breeding oysters in a similar manner to *Coscinodiscus wailesii* (see above).

**Dinophyceae**

*Alexandrium minutum* Halim

This toxic, warm-water species has its main dispersal area in the coastal waters of the Mediterranean Sea, Taiwan, New Zealand and Australia (e.g. Hallegraeff *et al.* 1988). In northern Europe, persistent blooms of *A. minutum* have occurred since 1985 along the north-western coast of Brittany, especially in small bays or shallow estuaries, causing severe losses to aquaculture (Nezan and Ledoux 1989). In 1987, a toxic bloom of this

kind occurred in the Irish coastal waters (Gross 1989). The first occurrence of *A. minutum* cells in Dutch waters in 1992 (TRIPPOS 1993) was probably a result of transport by water currents through the English Channel into the southern North Sea. So far, no observations have been reported from the southern North Sea, especially from the German Bight, but *A. minutum* was found on the coast of Norway, and there is a report of living resting cysts from the western Baltic Sea (Nehring 1994b). An exact delineation of its north European dispersal area cannot yet be made as the identification of the tiny inconspicuous *A. minutum* is made even more difficult by the fact that the first apical plate of the vegetative cells may vary in appearance. Moreover, the species *A. ibericum* is considered to be a synonym for *A. minutum*, as is *A. lusitanicum* (Franco *et al.* 1995).

#### *Gymnodinium catenatum* Graham

Live resting cysts of this potentially toxic species were observed for the first time in northern Europe in 1987 in the Kattegat (Ellegaard *et al.* 1993). In the German Bight, live cysts have been found since 1992 (Nehring 1995). In the Dutch Wadden Sea live cysts as well as vegetative cells were observed in 1991 (Peperzak *et al.* 1996). There is evidence that the occurrence of this thermophilic species is connected with transport by ocean currents from southern European waters (Nehring 1995). At present the taxonomic status of the northern *G. catenatum* is under discussion because the vegetative cells and also the cysts show small morphological variations from those found in northern Spain. To solve this problem, genetic analysis of *G. catenatum* from different parts of the world is being carried out, but at present no results are available. However, it is a fact that before 1983 the distinctive vegetative cells and living cysts of the northern *G. catenatum* had never been reported in any of the numerous plankton and cyst investigations in North Europe (see Nehring 1995).

#### *Gymnodinium chlorophorum* Elbrächter and Schnepf

In August 1990, this species caused an unusual green-coloured bloom in the German Bight (Anonymous 1991; Nehring *et al.* 1995). The same species (described as *Gyrodinium* sp. 1982) developed a bloom in summer 1989 near the mouth of the River Loire (France), with more than 60 million cells per litre (Sournia *et al.* 1992). Cells probably drifted along the French Atlantic coast, through the English Channel and into the German Bight, where they may have initiated the above-mentioned bloom in 1990.

#### *Gyrodinium aureolum* Hulburt

The species *Gyrodinium aureolum* from the western North Atlantic, which was described by Hulburt (1957), was first recorded in 1966 by Braarud and Heimdal (1970) on the SW coast of Norway. Here it caused the decay of bottom dwelling animals and a major fish kill. Its initial appearance in Europe may have been due to ballast water. Several other toxic outbreaks followed (e.g. 1968 off the Danish coast and 1976 off the Norwegian coast, Hansen and Sarma 1969; Tangen 1977). In 1968 a bloom of *G. aureolum* (described as *Gymnodinium* sp.) occurred in the German Bight near Helgoland, but no toxic

effects were observed (Hickel *et al.* 1971). *G. aureolum* has also been observed in high numbers in the English Channel, especially where fronts occur (Boalch 1987). More recently, the taxonomic affinity between the European *G. aureolum* and the North American specimen has been questioned (Partensky *et al.* 1991). It seems that the European specimens show a stronger similarity to *Gymnodinium mikimotoi* (synonym *G. nagasakiense*), a toxic bloom-forming species from the Pacific (*e.g.* Takayama and Adachi 1984), than to the original description of *G. aureolum* by Hulburt (Steidinger and Tangen 1996). Also immunochemical studies have shown that the European *G. aureolum* and *G. mikimotoi* cannot be distinguished from each other (Vrieling *et al.* 1995a). However, the real taxonomic status of the European *G. aureolum* remains unclear. Immunochemical results given by Blasco *et al.* (1996) suggest that the American *G. aureolum* and the European one, might simply be different morphotypes of the same species. More work needs to be done on studying the genetic fingerprinting of isolates of the *G. aureolum* complex from different parts of the world.

#### *Prorocentrum redfieldii* Bursa

Since 1961 there have been reports of this distinctive dinoflagellate from the Dutch Wadden Sea, where it has developed blooms of up to 1.4 million cells per litre (Kat 1979). Since 1992 this species has frequently been found in the German Wadden Sea (Elbrächter 1994). *P. redfieldii* is often referred to in the literature by its synonym *P. triestinum* and is considered to be a neritic brackish-water species (Bursa 1959). Since it is pandemic, nothing can be said about the possible pathway into northern Europe.

#### *Raphidophyceae*

##### *Chattonella antiqua* Ono; *Chattonella marina* Hara and Chihara

These two *Chattonella* species, which are also able to form cysts during their life cycle, are known for the toxic blooms they have produced in Japanese waters (Fukuyo *et al.* 1990). In Europe, they have only been found in the Dutch Wadden Sea, where they have been regularly recorded since 1991 (TRIPOS 1993). In 1993 and 1994, minor blooms ( $10^5$  cells per litre) of *C. marina* developed here, but without toxic effects (TRIPOS 1994; Vrieling *et al.* 1995b). Future studies aim to show which pathway these species took and whether they will spread further in the North Sea. Possibly, as in the case of dinoflagellates, surveying sediments for the presence of cysts could be helpful.

##### *Fibrocapsa japonica* Toriumi and Takano

This cyst-forming species, which is common all over the world in warmer waters, first appeared in northern Europe in the Dutch Wadden Sea in 1991 (Vrieling *et al.* 1995b). Toxin analysis of the Dutch strain showed that *F. japonica* produced a neurotoxin which was toxic to fish (Khan *et al.* 1996). Since 1992, it has also been found in the German Wadden Sea (Elbrächter 1994). *F. japonica* was also observed some years ago on the French coast (Billard 1992 cited in Vrieling *et al.* 1995b). This species can only be identified reliably from living organisms, so the exact time of its first occurrence in northern Europe

cannot be determined precisely. In the Wadden Sea areas of the North Sea, where living samples have been analysed under monitoring programmes since 1966, this species seems to have only established populations in the past few years. Again for *F. japonica*, cysts might help to clarify which pathway this species took.

### *Heterosigma akashiwo* Hada

This toxic, cyst-forming species was first found in the Dutch Wadden Sea in 1992 (TRIPOS 1993). In 1994, *H. akashiwo* developed minor blooms here with more than  $10^6$  cells per litre, but without toxic effects (Rademaker *et al.* 1995). In the German Wadden Sea, *H. akashiwo* was found relatively frequently during 1993 (Elbrächter 1994). It has also recently been observed in Danish waters. In the literature *H. akashiwo* is often referred to as its synonym *H. carterae*. This species attracted attention mainly by its toxic blooms in waters around Japan and New Zealand (Fukuyo *et al.* 1990), although a bloom was also observed in summer 1988 near the Faeroe Islands (Morris 1989). However, the limits of its distribution are as yet uncertain, as it is frequently confused with *Olisthodiscus luteus*. Due to this taxonomic uncertainty, the reports of "*O. luteus*" in 1964 in the Oslo Fjord by Braarud (1969 cited in Lassus 1988) and at a later date on the Belgian North Sea coast (Reid *et al.* 1990) are not definite. As *H. akashiwo* decomposes relatively quickly in fixed samples, it is not possible to prove the exact time of its first occurrence in northern Europe. The situation is different for the Wadden Sea areas of the North Sea, where living samples have been analysed in monitoring programmes prior to 1992. This species seems to have established itself in the southern North Sea only in the past few years. Cyst distribution may help to clarify this question.

## Conclusion

Planktonic organisms by nature drift passively with the water masses. They can be transported over long distances, as has long been recognised (Fraser 1962; Russell 1935). Other pathways for migration into new areas are transport *e.g.* by birds, in the ballast water of ships or as a result of aquaculture. In the North Sea, the successful colonization of planktonic organisms introduced by each of these immigration pathways could be proven (Figure 1). However, considering the water volumes moved over the decades and the diversity of algae contained therein the infection rate is relatively low (for the German Bight reflecting an overall increase in phytoplankton species of about 1 %).

The factors which enable alien species to establish populations cannot be easily identified. The number of influential factors is high and the significance of single parameters varies from one species to another. Besides chemical factors *e.g.* changes in nutrient or trace-substance input, there are numerous physical factors which may be closely related to climate. The direct dependence of marine organisms on water temperature seems to make global warming the decisive parameter for climate-induced changes in species composition, especially in the North Sea (Nehring 1998). This assumption is based on the observed recent establishment of warm water species (*e.g.* *Alexandrium minutum*, *Rhizosolenia indica*, *Stephanopyxis palmeriana*), which could not have previously survived.

How far the establishment of new phytoplankton species influences the nutrient cycles in the North Sea ecosystem can only be answered in some isolated details. These include *e.g.* the repression of indigenous species, the negative and also the positive effects on grazing organisms, damage to marine fauna and shellfish poisoning by toxin release, or the aesthetic problems of water quality (*e.g.* Rick and Dürselen 1995; Hesse *et al.* 1996).

## References

- Anderson, D.M., 1995: Identification of harmful algal species using molecular probes: an emerging perspective. In: Lassus, P.; Arzul, G.; Erard, E.; Gentien, P.; Marcaillou, C. (eds.): Harmful Marine Algal Blooms. Paris: Lavoisier, p. 3–13.
- Anonymous, 1991: Report of the mass development of the "Y-100" alga in the German Bight. Red Tide Newsl. 4(1): 12–14.
- Atkinson, K.M., 1972: Birds as transporters of algae. Br. Phycol. J. 7: 319–321.
- Atkinson, K.M., 1980: Experiments in dispersal of phytoplankton by ducks. Br. Phycol. J. 15: 49–58.
- Blasco, D.; Bérard-Therriault, L.; Levasseur, M.; Vrieling, E.G., 1996: Temporal and spatial distribution of the ichthyotoxic dinoflagellate *Gyrodinium aureolum* Hulburt in the St Lawrence, Canada. J. Plankton Res. 18: 1917–1930.
- Boalch, G.T., 1987: Recent blooms in the western English channel. Rap. P.-v. Réunion. Cons. int. Explor. Mer 187: 94–97.
- Boalch, G.T.; Harbour, D.S., 1977: Unusual diatom off the coast of south-west England and its effect on fishing. Nature (Lond.) 269: 687–688.
- Braarud, T.; Heimdal, B.R., 1970: Brown water on the Norwegian coast in autumn 1966. Nytt. Mag. Bot. 17: 91–97.
- Breemen, P.J. van, 1906: Bemerkungen über einige Planktonformen. Verhand. Rijksinst. Onderzoek der Zee 1: 1–7.
- Bursa, A., 1959: The genus *Prorocentrum* Ehrenberg. Morphodynamics, protoplasmatic structures, and taxonomy. Can. J. Bot. 37: 1–31.
- Cadée, G.C.; Hegemann, J., 1991: Phytoplankton and primary production, chlorophyll and species composition, organic carbon and turbidity in the Marsdiep in 1990, compared with foregoing years. Hydrobiol. Bull. 25: 29–35.
- Carlton, J.T., 1989: Man's role in changing the face of the ocean: biological invasions and implications for conservation of nearshore environments. Conserv. Bull. 3: 265–273.
- Carlton, J.T.; Geller, J.B., 1993: Ecological roulette: the global transport of nonindigenous marine organisms. Science 261: 78–82.
- Cleve, P.T., 1887: A treatise on the phytoplankton of the Atlantic and its tributaries. Uppsala: 27 pp.
- Cleve, P.T., 1900: The plankton of the North Sea, the English Channel and the Skagerrak. K. Svensk. Vet.-Akad. Handl. 32(8): 1–53.
- Dale, B.; Madsen, A.; Nordberg, K.; Thorsen, T.A., 1993: Evidence for prehistoric and historic "blooms" of the toxic dinoflagellate *Gymnodinium catenatum* in the Kattegat-Skagerrak re-

- gion of Scandinavia. In: Smayda, T.J.; Shimizu, Y. (eds.): Toxic Phytoplankton Blooms in the Sea, Developments in Marine Biology 3. Amsterdam: Elsevier, p. 47–52.
- Drebes, G., 1974: Marines Phytoplankton - Eine Auswahl der Helgoländer Planktonalgen (Diatomeen, Peridineen). Stuttgart: G. Thieme. 186 pp.
- Drebes, G., 1991: Neue Planktondiatomeen im Sylter Wattenmeer. Jahresber. Biol. Anst. Helgol. 1990: 29–30.
- Drebes, G.; Elbrächter, M., 1976: A checklist of planktonic diatoms and dinoflagellates from Helgoland and List (Sylt), German Bight. Bot. Mar. 19: 75–83
- Elbrächter, M., 1994: Phytoplankton und toxische Algen im Wattenmeer. In: Lozán, J.L.; Rachor, E.; Reise, K.; Westernhagen, H. v.; Lenz, W. (eds.): Warnsignale aus dem Wattenmeer. Berlin: Blackwell, p. 81–86.
- Elbrächter, M., 1995: Phytoplankton: Besiedlungsstrategien der Wasserkörper und Transportmechanismen. List: Abschlußbericht SWAP Teilprojekt 1.5. 70 pp.
- Ellegaard, M.; Christensen, N.F.; Moestrup, Ø., 1993: Temperature and salinity effects on growth of a non-chain-forming strain of *Gymnodinium catenatum* (Dinophyceae) established from a cyst from recent sediments in the Sound (Øresund), Denmark. J. Phycol. 29: 418–426.
- Eno, N.C.; Clark, R.A.; Sanderson, W.G., 1997: Non-native marine species in British waters: a review and directory. Peterborough: Joint Nature Conservation Committee. 152 pp.
- Franco, J.M.; Fraga, S.; Zapata, M.; Bravo, I.; Fernández, P.; Ramilo, I., 1995: Comparison between different strains of the genus *Alexandrium* of the *minutum* group. In: Lassus, P.; Arzul, G.; Erard, E.; Gentien, P.; Marcaillou, C. (eds.): Harmful Marine Algal Blooms. Paris: Lavoisier, p. 53–58.
- Fraser, J., 1962: Nature Adrift – The Story of Marine Plankton. London: Foulis. 128 pp.
- Fukuyo, Y.; Takano, H.; Chihara, M.; Matsuoka, K. (eds.) 1990: Red Tide Organisms in Japan - An Illustrated Taxonomic Guide. Tokyo: Uchida Rokakuho. 430 pp.
- Gieskes, W.W.; Kraay, G.W., 1986: Analysis of phytoplankton pigments by HPLC before, during and after mass occurrence of the microflagellate *Corymbellus aureus* during the spring bloom in the open northern North Sea in 1983. Mar. Biol. 92: 45–52.
- Gran, H.H., 1908: Diatomeen. In: Brandt, K.; Apstein, C. (eds.): Nordisches Plankton, Botanischer Teil XIX. Kiel and Leipzig: Lipsius und Tischer. 146 pp.
- Gross, J., 1989: Re-occurrence of red tide in Cork Harbour, Ireland. Red Tide Newsl. 2(3): 4–5.
- Hagmeier, E., 1992: Zum Auftreten der Kieselalge *Coscinodiscus wailesii* im Sommer 1991. Jahresber. Biol. Anst. Helgol. 1991: p. 46.
- Hallegraeff, G.M.; Steffensen, D.A.; Wetherbee, R., 1988: Three estuarine Australian dinoflagellates that can produce paralytic shellfish toxins. J. Plankton Res. 10: 533–541.
- Hansen, V.; Sarma, A.H.V., 1969: On a *Gymnodinium* red water in the eastern North Sea during autumn 1968 and accompanying fish mortality with notes on the oceanographic conditions. Int. Counc. Explor. Sea, C.M./21: 1–10.
- Hasle, G.R., 1983: *Thalassiosira punctigera* (Castr.) comb. nov., a widely distributed marine planktonic diatom. Nord. J. Bot. 3: 593–608.
- Hasle, G.R.; Fryxell, G.A., 1977: The genus *Thalassiosira*, some species with a linear areola array. Nova Hedwigia (Beih.) 54: 15–66.

- Hasle, G.R.; Lange, C.B.; Syvertsen, E.E., 1996: A review of *Pseudo-nitzschia*, with special reference to the Skagerrak, North Atlantic, and adjacent waters. *Helgoländer Meeresunters.* 50: 131–175.
- Hesse, K.-J.; Tillmann, U.; Nehring, S.; Brockmann, U., 1996: Specific factors controlling phytoplankton distribution in coastal waters of the German Bight (North Sea). In: Eleftheriou, A.; Ansell, A.D.; Smith, C.J. (eds.): *Biology and Ecology of Shallow Coastal Waters*. Fredensborg: Olsen & Olsen, p. 11–22.
- Hickel, W.; Hagmeier, E.; Drebes, G., 1971: *Gymnodinium* blooms in the Helgoland Bight (North Sea) during August 1968. *Helgoländer wiss. Meeresunters.* 22: 401–416.
- Hulburt, E.M., 1957: The taxonomy of unarmored Dinophyceae of shallow embayments on Cape Cod, Massachusetts. *Biological Bull. (Woods Hole)* 112: 196–219.
- Kat, M., 1979: The occurrence of *Prorocentrum* species and coincidental gastrointestinal illness of mussel consumers. In: Taylor, D.L.; Seliger, H.H. (eds.): *Toxic Dinoflagellate Blooms*. Amsterdam: Elsevier, p. 215–220.
- Kat, M., 1982: Effects of fluctuating salinities on the development of *Thalassiosira angustii*, a diatom not observed before in the Dutch coastal area. *J. Mar. Biol. Ass. U.K.* 62: 483–484.
- Khan, S.; Arakawa, O.; Onoue, Y., 1996: Neurotoxin production by a chloromonad *Fibrocapsa japonica* (Raphidophyceae). *J. World Aquacult. Soc.* 27: 254–263.
- Kühn, S.F.; Drebes, G.; Schnepf, E., 1996: Five new species of the nanoflagellate *Pirsonia* in the German Bight, North Sea, feeding on planktic diatoms. *Helgoländer Meeresunters.* 50: 205–222.
- Lassus, P., 1988: *Plancton toxique et plancton d'eaux rouges sur les côtes européennes*. Brest: IFREMER. 111 pp.
- Makarova, I.V., 1970: Ad taxonomian specierum nonnullarum generis *Thalassiosira* Cl. Novit. *Syst. Plant. non Vasc.* 7: 13–20.
- Morris, J.E.M., 1989: Reports on Algal blooms - Faroes Islands. *Red Tide Newsl.* 2(1): p. 1.
- Nehring, S., 1993: Mortality of dogs associated with a mass development of *Nodularia spumigena* (Cyanophyceae) in a brackish lake at the German North Sea coast. *J. Plankton Res.* 15: 867–872.
- Nehring, S., 1994a: *Scrippsiella* spp. resting cysts from the German Bight (North Sea): A tool for more complete check-lists of dinoflagellates. *Neth. J. Sea Res.* 33: 57–63.
- Nehring, S., 1994b: First living *Alexandrium minutum* resting cysts in Western Baltic. *Harmful Algae News, UNESCO IOC Newsl.* 9: 1–2.
- Nehring, S., 1995: *Gymnodinium catenatum* Graham (Dinophyceae) in Europe: A growing problem? *J. Plankton Res.* 17: 85–102.
- Nehring, S., 1996: Recruitment of planktonic dinoflagellates: importance of benthic resting cysts and resuspension events. *Int. Rev. Gesamt. Hydrobiol.* 81: 513–527.
- Nehring, S., 1997: Dinoflagellate resting cysts from Recent German coastal sediments. *Bot. Mar.* 40: 307–324.
- Nehring, S., 1998: Establishment of thermophilic phytoplankton species in the North Sea - biological indicators for climatic changes? *Int. Council. Explor. Sea, J. Mar. Sci.* 55: 818–823.
- Nehring, S.; Hesse, K.-J.; Tillmann, U., 1995: The German Wadden Sea: A problem area for nuisance blooms? In: Lassus, P.; Arzul, G.; Erard, E.; Gentien, P.; Marcaillou, C. (eds.): *Harmful Marine Algal Blooms*. Paris: Lavoisier, p. 199–204.

- Nezan, E.; Ledoux, M., 1989: Red tide by *Alexandrium minutum* in France. Red Tide Newsl. 2(1): 2–3.
- Ostenfeld, C.H., 1908: On the immigration of *Biddulphia sinensis* Grev. and its occurrence in the North Sea during 1903–1907 and on its use for the study of the direction and rate of flow of the currents. Medd. Komm. Havunders. Ser. Plankton 1(6): 1–44.
- Partensky, F.; Gentien, P.; Sournia, A., 1991: *Gymnodinium* cf. *nagasakiense* = *Gyrodinium* cf. *aureolum* (Dinophycées). In: Sournia, A. (ed.): Le phytoplancton nuisible des côtes de France, de la biologie à la prevention. Brest: IFREMER, p. 63–82
- Paulsen, O., 1908: Peridinales. In: Brandt, K.; Apstein, C. (eds.): Nordisches Plankton, Botanischer Teil XVIII. Kiel and Leipzig: Lipsius und Tischer. 124 pp.
- Peperzak, L.; Verreussel, R.; Zonneveld, K.A.F.; Zevenboom, W.; Dijkema, R. 1996: The distribution of flagellate cysts on the Dutch continental shelf (North Sea) with emphasis on *Alexandrium* spp. and *Gymnodinium catenatum*. In: Yasumoto, T.; Oshima, Y.; Fukuyo, Y. (eds.): Harmful and Toxic Algal Blooms. Paris: UNESCO, p. 169–172.
- Rademaker, M.; Janmaat, L.; Zevenboom, W.; Jong, B. de, 1995: Potentially toxic algae along the Dutch coast in 1994. Harmful Algae News. UNESCO IOC Newsl. 10/11: p. 2.
- Reid, P.C.; Lancelot, C.; Gieskes, W.W.C.; Hagmeier, E.; Weichardt, G., 1990: Phytoplankton of the North Sea and its dynamics: A review. Neth. J. Sea Res. 26: 295–331.
- Rick, H.-J., 1990: Ein Beitrag zur Abschätzung der Wechselbeziehung zwischen den planktischen Primärproduzenten des Nordseegebietes und den Schwermetallen Kupfer, Zink, Cadmium und Blei auf der Grundlage von Untersuchungen an natürlichen Planktongemeinschaften und Laborexperimenten mit bestandsbildenden Arten. Aachen: Dissertation, RWTH. 330 pp.
- Rick, H.-J.; Dürselen, C.-D., 1995: Importance and abundance of the recently established species *Coscinodiscus wailesii* Gran and Angst in the German Bight. Helgoländer Meeresunters. 49: 355–374.
- Rincè, Y.; Plaumier, G., 1986: Données nouvelles sur la distribution de la diatomée marine *Coscinodiscus wailesii* Gran et Angst (Bacillariophyceae). Phycologia 25: 73–79.
- Russell, F.S., 1935: On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. J. mar. biol. Ass. U.K. 20: 309–331.
- Smith, V.H., 1983: Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221: 669–671.
- Steidinger, K.A.; Tangen, K., 1996: Dinoflagellates. In: Tomas, C.R. (ed.): Identifying Marine Diatoms and Dinoflagellates. London: Academic Press, p. 387–570.
- Sournia, A.; Bellin, C.; Billard, C.; Catherine, M.; Erard-Le Denn, E.; Fresnel, J.; Lassus, P.; Pastoureaud, A.; Soulard, R., 1992: The repetitive and expanding occurrence of a green, bloom-forming dinoflagellate (Dinophyceae) on the coasts of France. Cryptogamie: Algol. 13: 1–13.
- Takayama, H.; Adachi, R., 1984: *Gymnodinium nagasakiense* sp. nov., a red tide forming dinophyte in the adjacent waters of Japan. Bull. Plankton Soc. Japan 31: 7–14.
- Tangen, K., 1977: Blooms of *Gyrodinium aureolum* (Dinophyceae) in North European waters, accompanied by mortality in marine organisms. Sarsia 63: 123–133.
- TRIPOS, 1993: Biomonitoring van fytoplankton in de Nederlandse zoute en brakke wateren 1992. Rijkswaterstaat Dienst Getijdewateren, Rapp. 1992.

- TRIPOS, 1994: Project algenbloei 1994. Rijkswaterstaat Directie Noordzee. Rapp. 1994/Projekt T001.
- Vrieling, E.G.; Gieskes, W.W.C.; Rademaker, T.W.M.; Vriezekolk, G.; Peperzak, L.; Veenhuis, M., 1995a: Flow cytometric identification of the ichthyotoxic dinoflagellate *Gyrodinium aureolum* in the central North Sea. In: Lassus, P.; Arzul, G.; Erard, E.; Gentien, P.; Marcaillou, C. (eds.): Harmful Marine Algal Blooms. Paris: Lavoisier, p. 743–748.
- Vrieling, E.G.; Koeman, R.P.T.; Nagasaki, K.; Ishida, Y.; Peperzak, L.; Gieskes, W.W.C.; Veenhuis, M., 1995b: *Chattonella* und *Fibrocapsa* (Raphidophyceae): First observation of potentially harmful, red tide organisms in Dutch coastal waters. Neth. J. Sea Res. 33: 183–191.
- Vrieling, E.G.; Koeman, R.P.T.; Peperzak, L.; Veenhuis, M.; Scheerman, P.; Gieskes, W.W.C., 1996: *Pseudo-nitzschia pungens* forma *multiseries* and other *Pseudo-nitzschia* species in the Dutch Wadden Sea. In: Yasumoto, T.; Oshima, Y.; Fukuyo, Y. (eds.): Harmful and Toxic Algal Blooms. Paris: UNESCO, p. 139–142.
- Wyatt, T., 1995: Global spreading, time series, models and monitoring. In: Lassus, P.; Arzul, G.; Erard, E.; Gentien, P.; Marcaillou, C. (eds.): Harmful Marine Algal Blooms. Paris: Lavoisier, p. 755–764.

### Acknowledgements

The constructive comments of Drs G.C. Cadée and G. Drebes were greatly appreciated.

**Author's address:** Dr. Stefan Nehring, Bundesanstalt für Gewässerkunde, Kaiserin-Augusta-Anlagen 15–17, D-56068 Koblenz, Germany. Fax: +49-(0)261-1306-5374, e-mail: nehring@bafg.de