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DINOFLAGELLATE RESTING CYSTS IN RECENT SEDIMENTS OF THE WESTERN BALTIC AS INDICATORS FOR THE OCCURRENCE OF "NON-INDIGENOUS" SPECIES IN THE WATER COLUMN

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Abstract. In sediment studies from Kiel Bight, Germany (Baltic Sea), nine dinoflagellate resting cysts were identified whose motile cells have not been officially recorded in the area up to now. These "non-indigenous" cysts are described using the theca-based classification. The wide distribution of living and empty cysts of *Gymnodinium catenatum*, *Peridinium dalei*, *Protoperidinium denticulatum* and *P. punctulatum* suggests that they are common members of the Western Baltic phytoplankton community. The cysts of *G. catenatum* as well as the record of living cysts of *Alexandrium minutum*, whose vegetative cells cause Paralytic Shellfish Poisoning in southern European coastal waters, may represent potential seedbeds for spontaneous toxic bloom initiation. The occurrence of *Diplopelta symmetrica*, *P. compressum*, *P. cf. excenticum* and *Scrippsiella lachrymosa* cysts may be related to bottom currents from the Kattegat area.

INTRODUCTION

Among the organisms which cause nuisance blooms, dinoflagellate species, which often include a dormant cyst stage (resting cyst) in their sexual life cycle, play an important role. Functionally, resting cyst-formation affects species dispersal, bloom initiation, bloom termination and survival during adverse conditions (Dale 1983). At present, more than seventy species of marine and more than twenty species of freshwater dinoflagellates are known to produce resting cysts (Nehring 1993 a). Laboratory experiments revealed that resting cysts behave as fine particles in the sedimentary regime and are thus concentrated by sedimentary processes (Dale 1976). Like their vegetative counterparts, cysts (new formed or resuspended) are chiefly transported with residual currents (Anderson *et al.* 1985) and may hence be indicators of water current systems (Nehring 1993 b). The role of such a transport mechanism of cysts in "hierarchical" dispersion of alien species received considerable attention (Nehring in press a).

Cyst studies are revealing a benthic view of dinoflagellate ecology and offer the possibility to overcome some difficulties presently limiting planktological studies based on discrete sampling, in providing time-integrated information on the whole water column (Hesse *et al.* in press). In addition, direct comparison of motile stages with those of their cysts showed that differences between many species are more distinct at the cyst level. For these reasons, cysts may indicate the presence of a species in the water column that has been previously overlooked or misclassified. Also, dinoflagellates may be identified after a toxic bloom using cyst analysis long after their motile stages have vanished from the water column.

This paper presents a description of dinoflagellate resting cysts isolated from recent sediments of Kiel Bight, whose motile cells are unknown for the area. Some factors which may influence the occurrence of these species are considered briefly.

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MATERIAL AND METHODS

In April 1993 (20.-21.93), undisturbed surface sediment samples of Kiel Bight (Table 1, Figure 1) were collected with a modified Meischner & Rumohr (1974) gravity corer from aboard RV "Littorina". For coarse sediments, a Box corer was used. Duplicate sediment cores (10 cm long, 2,6 cm diameter) were obtained from the corers and stored in the dark at 4°C until further examination.

Core subsamples were disaggregated by probe-sonication (Bransonic 52) to separate the cysts from organic and inorganic aggregates. The sonicated suspension was poured through a 150 mm gauze and accumulated on a 20 mm gauze. The residue on the 20 mm gauze was rinsed from the net and resuspended in 30 ml of filtered seawater. This 30 ml preparation was examined in entirety by 500 µl aliquots on Utermöhl

Table 1. Position, water depth and sediment characteristics of Kiel Bight stations

Station	Name	Coordinates	Water depth	Sampling date	Sediment type
L1	Tonne Kiel 1	54°21,60'N 10°09,80'E	13 m	21.04.93	mud
L2	Klever-berg	54°27,50'N 10°14,70'E	20 m	21.04.93	mud
L3	Kieler Tief	54°29,20'N 10°19,40'E	19 m	21.04.93	mud
L4	Gabels-flach	54°31,90'N 10°21,00'E	11 m	21.04.93	sand
L5	Boknis Eck	54°32,10'N 10°02,50'E	24 m	21.04.93	muddy sand
L6	Dorsch-mulde	54°37,25'N 10°18,60'E	21 m	20.04.93	mud
L7	Kieler Bucht	54°36,09'N 10°26,88'E	18 m	20.04.93	sandy mud
L8	Süder-fahrt	54°32,45'N 10°44,39'E	22 m	20.04.93	mud
L9	Flügge-sand	54°29,10'N 10°55,00'E	11 m	20.04.93	mud

slides using a Zeiss Axiovert inverted microscope.

For reference, individual cysts were picked out from Utermöhl slides and placed on microscopic slides with glycerine jelly as the mounting medium in a seal of wax.

Some individual cysts were used for germination experiments in order to identify species by their motile thecate stage. These cysts were isolated microscopically using a micropipette and washed twice in filtered seawater. The cysts were placed in small sterile incubation chambers (Corning Cell Wells) containing filtered seawater of the sample location (Salinity 15.6 ‰) or medium f/2 (Guillard, Ryther 1962) and incubated for a period of up to 14 days under natural light conditions at room temperature (~18°C).

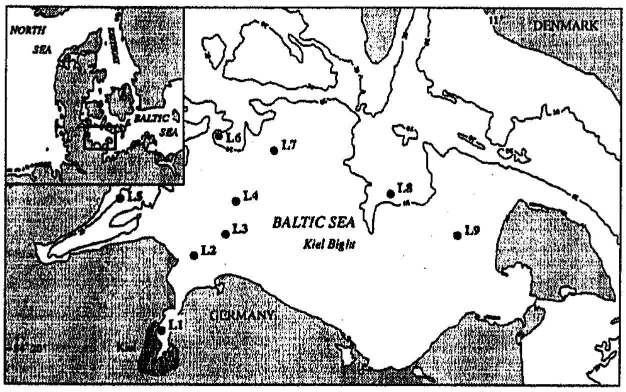

Figure 1. Study area - the Kiel Bight (Baltic Sea) with location of stations investigated.

RESULTS

The comprehensive cyst survey in Kiel Bight reveals that living and empty cysts are widespread throughout the investigated stations. Altogether 25 cyst types were identified to species level (see Nehring in press b) whereby the motile cells of 9 species have not been officially recorded in the area so far.

Many dinoflagellate cysts have dual nomenclature, i.e. that the of cyst (palynological) and that of the vegetative stage (biological). In this paper, cysts of "non-indigenous" species will be described using biological nomenclature, although the palynological name is included for reference if available.

Alexandrium minutum Halim
Figure 2A, B
Erard-Le Denn et al. (1993), p. 110, fig. 2

Cysts are circular in apical view (21-25 µm in diameter) and reniform in lateral view (22 x 28 µm). The clear cyst wall is lightly covered with mucilage. A prominent orange-red accumulation body is present.

Remarks: The cyst of *A. minutum* differs from the cysts of other *Alexandrium* species in its shape (Bolch *et al.* 1991). At present this cyst type is known in Europe only from recent marine sediments of northern France (Erard-le Denn *et al.* 1993). In the present study, germination experiments were not successful.

Occurrence: Living cysts (L5)

Diplopelta symmetrica Pavillard
Figure 2C
Dale et al. (1993), p.131, fig.5-8, 16, 17

Brown, spherical to ovoidal cyst (40-45 µm in diameter) with a thick wall which is densely covered by thin (hair-like) processes (1-4 µm long). The archeopyle is a slit (theropylic type sensu Matsuoka 1985).

Remarks: The unequivocal cyst of *D. symmetrica* was first described by Dale *et al.* (1993) from the Oslofjord and from a Italian Lagoon. In Kiel Bight sediments, only empty cysts were found.

Occurrence: Empty cysts (L8)

Gymnodinium catenatum Graham
Figure 2D
Bolch, Hallegraeff (1990), p.186, figs.33a-c

Brown, spherical cyst (30-35 µm diameter) with globular contents. A prominent red accumulation body is present. The cyst surface is micro-reticulated and reflects the girdle, the sulcus and the apical groove of the vegetative cell. The archeopyle is a long slit along the paracingulum (chasmic type sensu Matsuoka 1985). Several empty cysts showed an additional step-like fracture on the slit.

Remarks: This cyst type is known in Europe from recent marine sediments of the Iberian peninsula and was recently reported for Northern Europe waters from the North Sea and the Kattegat area (Ellegaard *et al.* 1993, Nehring 1993 b). Cysts of the North Sea, Kattegat and Kiel Bight are slightly smaller (30-40 µm vs. 37-60 µm) than those described from other parts of the world (see Nehring in press a). *G. catenatum* is known to form characteristic snake-like chains consisting of up to 64 single individuals (Blackburn *et al.* 1989). All germinated specimens from Kiel Bight produced not more than two cell pairs.

Occurrence: Living cysts (L5, L6, L7, L8)
Empty cysts (L3, L5, L6, L7, L8)

Peridinium dalei (Indelicato & Loeblich) Balech
Figure 2E
Lewis (1991), p.95, 96, figs. 10-16

Cysts are spherical or slightly subspherical (20-28 µm diameter excl. spines; spines length 2-5 µm) and a red accumulation body is often visible. The cyst wall is clear and the archeopyle is a simple split. Normally, numerous spines are developed, but Kiel Bight specimen showed a clear tendency for progressive reduction of process-length, compared with specimens from the North Sea (Nehring in press a).

Remarks: Reduction of process-length in Baltic Sea specimens was observed by Nehring (in press b) also for *Gonyaulax polyedra* and *Protoceratium reticulatum* and interpreted as an impact of salinity on cyst morphology. Similar observations were made by Wall *et al.* (1973) in low salinity assemblages from late Quaternary sediments in the Black Sea. In present study, most cysts germinated.

Occurrence:
Living cysts (L1, L2, L3 L4, L5, L6, L7, L8)
Empty cysts (L1, L2, L3, L4, L5, L6, L7, L8)

Protoperidinium compressum (Abé) Balech
Figure 2F
(Palinological taxon: Stelladinium stellatum (Wall) Reid)
Reid (1977), p.443, pl.2 figs. 19, 20

Dorso-ventrally compressed pale brown cyst (28-32 µm wide, horns excluded) with smooth wall and unique stellate morphology. The cyst carries 5 horns, one apical, two antapical and two lateral horns, which are long (up to 22 µm), solid and needle-shaped. The archeopyle is on the anterior dorsal surface and formed by loss of the 2a intercalary paraplate.

Remarks: The unequivocal cyst of *P. compressum* differs from *S. reidii* cysts (Bradford 1975) in its smaller

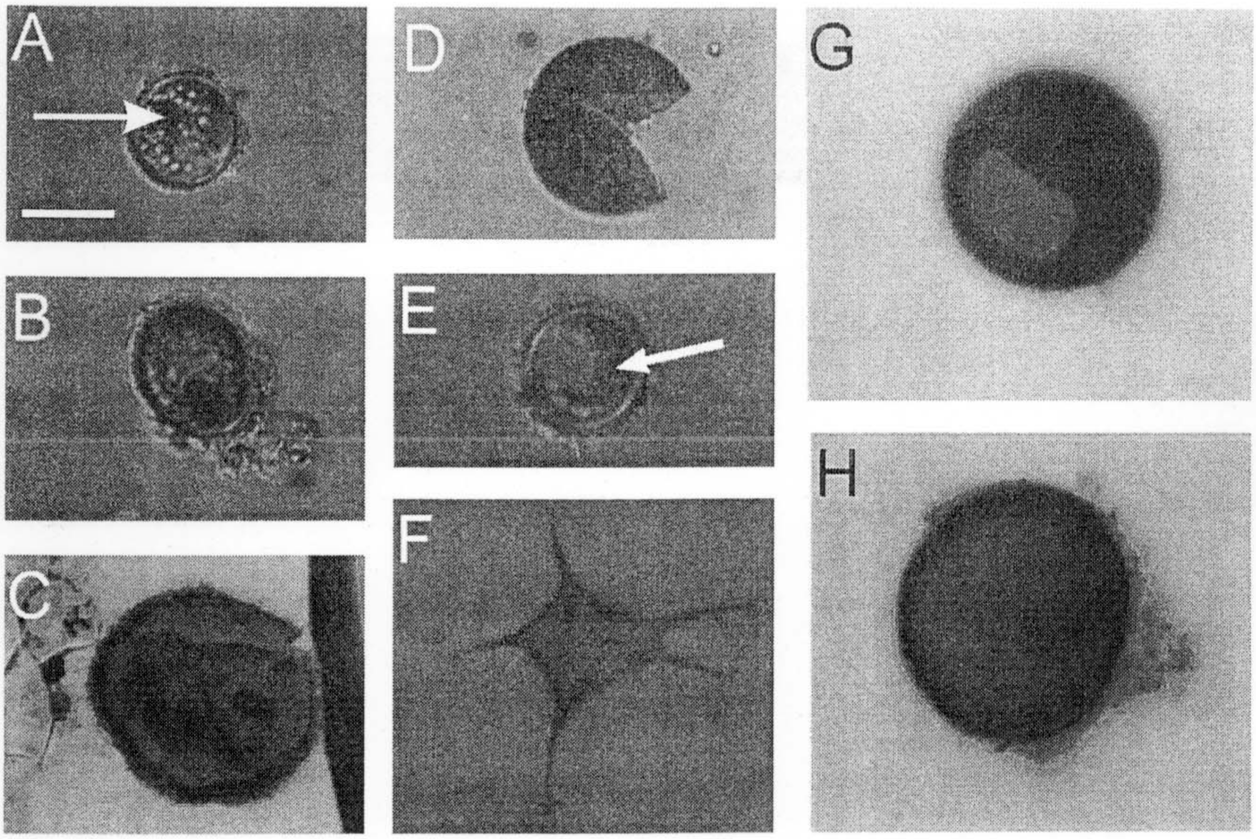

Figure 2. Resting cysts of dinoflagellates isolated from recent Baltic Sea sediments, which do not have vegetative cells indigenous from this region. A - B: *Alexandrium minutum,* A: Living cyst with red accumulation body (arrow), apical view; B: living cyst, lateral view. C: Cyst of *Diplopelta symmetrica* with hair-like processes. D: *Gymnodinium catenatum,* cyst split open (chasmic type of archeopyle) roughly around one edge of paracingulum. E: Cyst of *Peridinium dalei* with red accumulation body (arrow). F: Empty cyst of *Protoperidinium compressum.* G: Empty cyst of *Protoperidinium denticulatum* showing hexagonal archeopyle. H: Apical view of empty cyst of *Protoperidinium* cf. *excentricum.* Scale bar: 18 µm in (A-E), 20 µm in (F-H).

size, solid processes and smaller archeopyle. Only empty cysts were found.

Occurrence: Empty cysts (L8)

Protoperidinium denticulatum (Gran & Braarud) Balech
Figure 2G
Wall & Dale (1968), p.277, pl. 3 fig. 30

Brown spherical cyst (40-45 μm diameter) with a smooth wall. The archeopyle is hexagonal, laterally elongated (shaped by two long sides which are slightly curved and four intermediate sides) and formed by the loss of the 2a intercalary paraplate.

Remarks: At present, the cyst and archeopyle morphology of round brown cysts does not reveal distinct criteria for species determination. Confusion with several other species forming very similar cysts is possible (see below, *P. punctulatum*). In the present study, one cyst germinated and was identified as *P. denticulatum*.

Occurrence:
Living cysts (L1, L2, L3, L4, L5, L6, L7, L8, L9)
Empty cysts (L3, L4, L5,L6, L7)

Protoperidinium cf. *excentricum* (Paulsen) Balech
Figure 2H
Lewis et al. (1984), p.26, 28, fig. 2h

Brown and smooth-walled cyst which is slightly dorsoventraly flattened (48 μm x 54 μm). An indented parasulcus is often visible. Cyst is sometimes enclosed by the parental theca.

Remarks: Ellegaard *et al.* (in press) found a similar cyst type in recent Kattegat sediments and identified it by germination experiments as *P. excentricum*. No specimen from Kiel Bight germinated.

Occurrence: Living cysts (L2, L7, L8)
Empty cysts (L5, L6, L7, L8)

Protoperidinium punctulatum (Paulsen) Belech
Figure 3A

Brown spherical cyst (52-62 μm in diameter) with a smooth wall. The archeopyle is hexagonal, laterally elongated (shaped by two long sides, one of which is curved, and two relatively long and two short intermediate sides) and formed by the loss of the 2a intercalary paraplate.

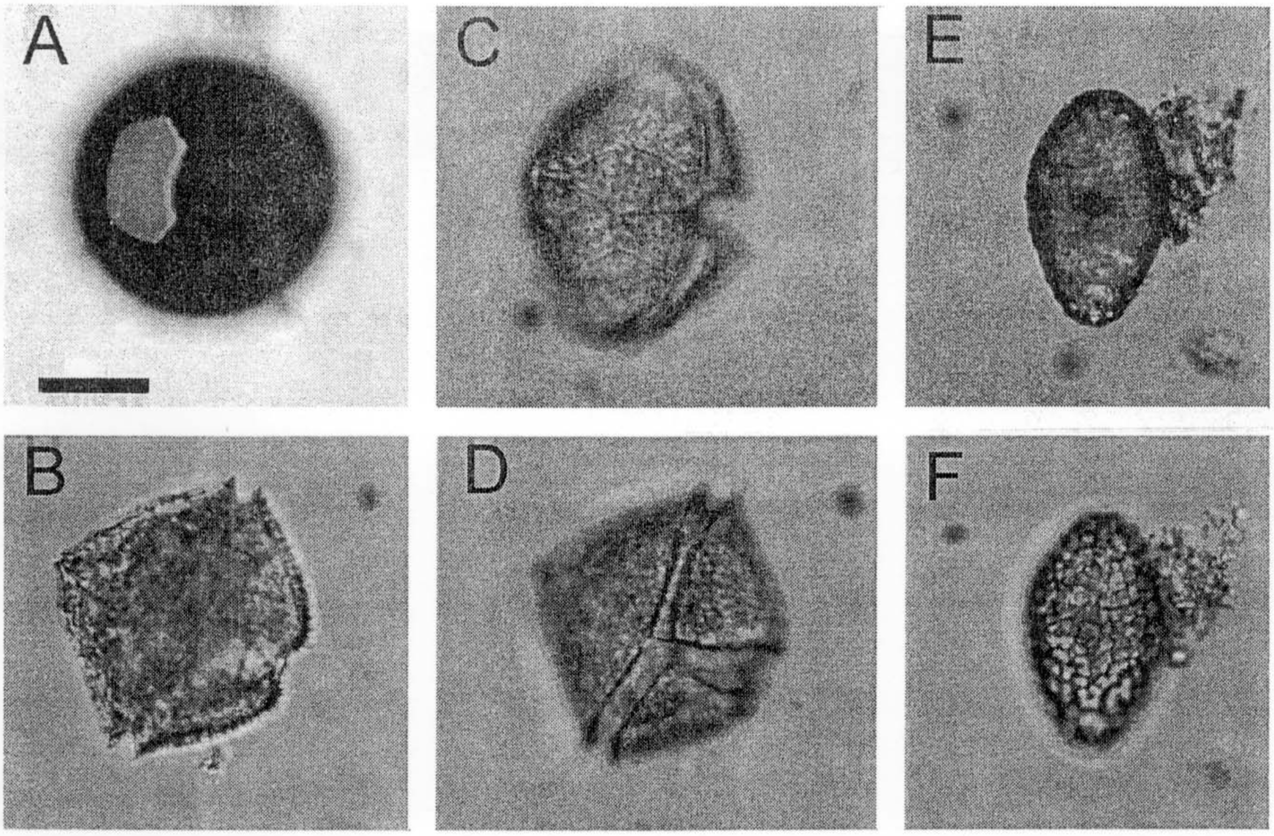

Figure 3. Resting cysts of dinoflagellates isolated from recent Baltic Sea sediments, which do not have vegetative cells indigenous from this region. A - D: *Protoperidinium punctulatum*, A: Empty cyst showing hexagonal archeopyle; B: excysted germling cell with spiny surface, optical cross section; C: Details of plate tubulation including the shape of the first apical plate (1'); D: Dorsal view showing the sulcal area and cingulum. E-F: *Scripsiella lachrymosa*, E: Empty cyst, optical cross section; F: Cyst showing calcareous ornament on surface. Scale bar: 18 μm in (A-F).

Remarks: germination of Kiel Bight specimens resulted in the unequivocal vegetative cells of *P. punctulatum* (Figure 3B-D). There were slight variations in the archeopyle of this species. Wall & Dale (1968) described the archeopyle of *P. punctulatum* as asymmetrical, specimens from Kiel Bight showed an symmetrical archeopyle. Round brown cysts have been a challenge to taxonomists or a long time. More critical work is required to elucidate this situation. After germination there is still confusion, as the thecate stages of *P. avellana, P. denticulatum, P.pundtulatum* and *P. thorianum* have very similar 2a plates (and cysts have hence similar archeopyles). Eventually cyst size may be a distinctive feature. however, this has not been confirmed.

Occurrence:

Living cysts (L1, L2, L3, L4, L5, L6, L7, L8, L9)
Empty cysts (L1, L2, L3, L4, L5, L6, L7, L8, L9)

Scrippsiella lachrymosa Lewis
Figure 3E, F
Lewis (1991), p.98, 99, fig. 30-32

Elongate oval cysts covered with thin, flattened calcareous plates which are jointly indented. The cyst is 37 to 47 µm long and 19 to 35 µm wide. In living cysts, a bright red accumulation body is visible (own observation on North Sea material). The archeopyle is a split towards one end of the cyst forming a cap shaped operculum and interpreted by Lewis (1991) as loss of paraplates 2'-4' and 1-3a.

Remarks: The unequivocal cyst of *S. lachrymosa* was first described by Lewis (1991) from Scottish Sea lochs and a similar cyst type was reported by Blanco (1989, p.800, Figure 5) as *S. trochoidea*, a largado from the Galician coast. Nehring (in press c) and Nehring *et al.* (in press) showed that the cyst of *S. lachrymosa* is a common member of the North Sea cyst flora. In Kiel Bight sediments only empty cysts were found.

Occurrence: Empty cysts (L8)

DISCUSSION

Studies on resting cysts are important for the understanding of many aspects of dinoflagellate ecology and biogeography (Dale 1983). Accumulations of cysts have been observed in a variety of marine ecosystems, including offshore trenches and depressions, fjords, estuaries and shallow coastal embayments (e.g. Baldwin 1987, Matsuoka 1987, Bolch & Hallegraeff 1990). However, only a few cyst studies were compared with extensive plankton records from overlying waters. For the area of the German Bight (North Sea), about 25 % of the locally occurring dinoflagellate species contribute cysts to bottom sentiments (Nehring 1994, in press c). However, Nehring (in press c) and Nehring *et al.* (in press) showed that the recent cyst flora in North Sea sediments contained several species whose motile forms had not been observed in the area up to now. In the case of the present study, the wide distribution of living empty cysts of *Gymnodinium catenatum, Peridinium dalei, Protoperidinium denticulatum* and *P. punctulatum* and the positive germination experiments with natural seawater from Kiel Bight suggest that these forms are common members of the Western Baltic phytoplankton community. In the area of Kiel Bight, altogether about 15 % of the locally occurring dinoflagellate species have developed resting cyst formation in their life cycle and used it actively (Nehring press b).

In France, since 1985, toxic algal blooms of the PSP-producing species *Alexandrium minutum* have occurred along the Brittany coast within small embayments or shallow estuaries (Nezan, Le Doux 1989). The cyst of *A. minutum* from Kiel bight conforms with the description and figure given by Erard-Le Denn *et al.* (1993) from the Brittany coast. The described occurrence of *Gymnodinium catenatum* cysts in Kiel Bight sediments is remarkable, because the present day distribution of vegetative cells of PSP-producing *G.catenatum* in European waters extends only to the Atlantic and Mediterranean coast of the Iberian peninsula (Estrada *et al.* 1984, Bravo *et al.* 1990) and is recorded from a Italian lagoon (Carrada *et al.* 1991). There are no reports of either species in any of the numerous investigations of living phytoplankton from northern European waters (Elbrächter pers. comm.). However, since March 1992, living *G. catenatum* cysts were found in increasing abundances in the German Bight (Nehring 1993 b, Nehring in press a, c), and were also recorded from recent sediments of the Danish coast bordering the Kattegat (Ellegaard *et al.* 1993).

The cyst of *G. catenatum* from Kiel Bight conforms with the specimen isolated from German Bight sediments and with the description given by Ellegaard *et al.* (1993) from the Kattegat area. Curiously, chain forming in the vegetative stage does not exceed more than two cells in the North Sea, Kattegat and Kiel Bight specimens. Recently, Paulmier (1992) described single cells and chains of two cells of a very similar and perhaps conspecific species (provisionally recorded as *G.* cf. *catenatum*) at the channel coast of France in 1983 and 1984. these findings suggest that the toxic *G. catenatum* was transported as cyst or motile cell by currents along the Atlantic coast of Spain and France.

The introduction of *A. minutum*, as well as *G. catenatum* to German coastal waters may be related to increase water influx through the English Channel into the North Sea (Becker, Dooley in press). The northward directed residual currents may have transported cells to the Skagerrak/Kattegat region. In January 1993, a massive salt water influx from the Kattegat through the Great Belt into the Western Baltic occurred (Anonymous 1993) and may have infected this area with *A. minutum* and *G. catenatum* cells. However, it is not yet sure wether the depicted scenario is true in the case of *A. minutum*, because resting cysts of this species were not detected in sediments of the German Bight (Nehring in press c) and the Kattegat area (Ellegaard *et al.* in press). As pointed out by Nering (in press d), it is quite possible that vegetative cells of the potentially toxic *A. minutum* have been overlooked in the plankton of the Western Baltic because of their small, inconspicuous shape and scarce occurrence. The positive germination experiments with *G. catenatum* in this study and by Ellagaard *et al.* (1993), which were conducted with natural sea water from the sample locations, show that also the occurrence of vegetative and potentially toxic *G. catenatum*, and possibly *A.minutum*, in Western Baltic waters is very likely. Phytoplankton monitoring programs must asses this problem.

The cyst of *Peridinium dalei* possesses unequivocal morphological features, whereas the vegetative stage is rather difficult to recognise by light microscopy because of its small size confusion with the closely related orthoperidinoid species (e.g. *Scrippsiella trochoidea*, which is a common species in the Western Baltic). It is suggested that due to these taxonomical difficulties, vegetative cells of P. dalei were overlooked in the region up to now.

Properidinium denticulatum and *P. punctulatum*, which are not known to occur as motile stages in the plankton of Kiel Bight, are present in adjacent North sea waters. these species are rather easy to identify even in preserved samples and it seems unlikely that they might have escaped observation. Their wide distribution as living and empty cysts in Kiel Bight sediments suggests that these forms are rather common in the phytoplankton community of the region, at least for delimited periods.

The main occurrence of cysts of *Protoperidinium cf. excentricum* in the deeper area of Kiel Bight may be a consequence of the reported salt water influx mentioned above, because both cysts and motile cells are common in the Kattegat area (Ellegaard *et al.* in press, Pankow 1990). Likewise, an import of empty cysts of *Diplopelta symmetrica*, *P.compressum* and *Scrippsiella lachrymosa* is suggested, because the former cyst type is known from Oslofjord (Dale *et al.* 193) both other cyst types are known from recent North Sea sediments (Nehring in press c) and *P.compressum* cysts from recent Kattegat sediments as well (Ellegaard *et al.* in press).

Cyst surveys provide a relatively inexpensive and easy way to obtain information about the occurrence of cyst-forming species. The benefits are increased if no historical phytoplankton data is available. Cyst studies offer a potential tool for early warning of the presence of a toxic species and future nuisance blooms in a given area (Ellegaard *et al.* 1993, Nehring 1993 b, Nehring in press d), since this information is not dependent on bloom periods. Recently, attention has been given to the possibility of dinoflagellate spread by transport of cysts via ships ballast water (Hallegraeff, Bolch 1991). Cyst studies, such as the present, merely show a relation of cyst distribution with water mass characteristics and current systems. In this way, areas hitherto free of algal problems may be infected with harmful species. In this context it is to be expected that changing water circulation as a result of climate change will bring about some surprising effects.

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