**Journal of Plankton Research** Vol.19 no.7 pp.937–956, 1997

# Interannual variability of PSP outbreaks on the north east UK coast

Ian Joint, Jane Lewis[1], James Aiken, Roger Proctor[2], Gerald Moore, Wendy Higman[1] and Margaret Donald[3]

*NERC Centre for Coastal and Marine Sciences, Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, [1]University of Westminster, School of Biological and Health Sciences, New Cavendish Street, London W1M 8JS, [2]NERC Centre for Coastal and Marine Sciences, Proudman Oceanographic Laboratory, Bidston, Merseyside L43 7RA and [3]MAFF Torry Research Station, PO Box 31, 135 Abbey Road, Aberdeen AB9 8DG, UK*

**Abstract.** Paralytic shellfish poisoning (PSP) occurs sporadically on the NE UK coast. The degree of toxicity shows considerable interannual variability, but particularly severe events occurred in 1968 and 1990. The time sequence of PSP toxin production in 1990 is described and compared with 1989 when no significant PSP toxin occurred. In 1990, PSP toxin was widespread in shellfish samples taken on 300 km of coastline, from Berwick to Whitby, and toxin was present at high concentrations for >1 month. The distribution of *Alexandrium tamarense* cysts in the sediments is described. High concentrations were found in the Firth of Forth and also in a number of regions offshore of the Scottish and English coasts. A water transport model has been used to estimate back trajectories, with the aim of determining the source of the *A.tamarense* bloom. The Firth of Forth has previously been suggested as the seed bed for *A.tamarense* outbreaks in the area, but the transport model clearly shows that *A.tamarense* moved inshore over a wide area in 1990; there was no single source of the bloom. Sea surface temperatures, estimated from satellite imagery, show that water temperatures were much higher at the end of April 1990, when the bloom occurred, than in 1989 when PSP toxin incidence was very low. These conditions would have resulted in early seasonal stratification and would have favoured phytoplankton growth in the water column.

## Introduction

The presence of toxic phytoplankton in coastal waters has significance for human health, with important economic implications through periodic closure of commercial shellfish fisheries. One of the most significant toxic algal outbreaks in the UK occurred in May 1968, when a number of cases of paralytic shellfish poisoning (PSP) were reported on the NE English coast. Only 10 outbreaks of shellfish poisoning have been recorded in the UK since 1828 (Ayres, 1975), but the 1968 incident was particularly serious and 78 people were hospitalized after eating mussels contaminated with PSP (Ayres and Cullum, 1978). The toxin-producing dinoflagellate bloom also had consequences for the coastal ecosystem, with large-scale deaths of seabirds and sand eels (Adams *et al.*, 1968; Coulson *et al.*, 1968).

The organism responsible for the poisoning was identified by Wood (1968) as the motile stage of the dinoflagellate, *Alexandrium tamarense* (named *Gonyaulax tamarensis* in 1968). The spatial distribution of the dinoflagellate in the offshore waters of the North Sea during this outbreak was mapped by the Continuous Plankton Recorder (CPR) Survey (Robinson, 1968). The cells of this phytoplankton are sufficiently large to be trapped by the mesh of the CPR and a retrospective analysis of samples taken by the CPR in the area suggested that *A.tamarense* first appeared in the Firth of Forth in mid-April and spread south-east, with maximum numbers occurring in the middle of May (Robinson, 1968).

Since the 1968 PSP event, the UK Ministry of Agriculture Fisheries and Food has regularly monitored shellfish for toxins; each year, in May and June, toxins have been found in shellfish harvested from the Moray Firth (57.4°N) to Bridlington (54.1°N) (Ayres, 1975). The degree of toxicity has varied from year to year, although subsequent outbreaks were much less severe than in 1968, and had a minimal impact on the shellfish industry. However, in May 1990, the routine monitoring procedures detected high concentrations of PSP in mussels and scallops from the NE English coast; as a consequence, a number of commercial shellfish fisheries were closed as a precautionary measure to protect public health.

This paper deals with questions relating to the appearance of *A.tamarense* in this region, the likely origin of a bloom and the environmental factors which influence phytoplankton growth. One particularly important question concerns the origin of the toxic phytoplankton assemblage; does the bloom develop from a seed population which originates in one part of the region, or is there a widespread and diffuse source? *Alexandrium* forms resting cysts which can be identified and quantified in marine sediments. Therefore, the distribution of *Alexandrium* cysts in the sediments of the region should indicate whether there are discrete areas of high cyst number which might act as sources of dinoflagellates that develop into nuisance blooms in the water column (e.g. Anderson and Keafer, 1985). The observations from the CPR Survey (Robinson, 1968) suggest that *Alexandrium* in the water column was most abundant in the Firth of Forth at the beginning of the outbreak. An initial cyst survey of the NE coastal region by Lewis *et al.* (1995) showed that cyst distribution was sporadic from Berwick to Flamborough Head, with lower concentrations occurring in sediments off the Scottish coast; however, numbers were consistently high within the Firth of Forth. Therefore, the Firth of Forth might be a seed bed, giving rise to motile populations, which are then spread throughout the region, largely through mixing by tides and currents. In this paper, further data are presented on cyst distribution to test the hypothesis that cyst numbers are elevated in the Firth of Forth.

We also test the suggestion that *Alexandrium* in the Firth of Forth can be transported south to influence the NE English coast. It is assumed that cysts or motile cells are introduced into the water column from the sediment surface in the early spring, and a depth-averaged tide plus surge model has been used to calculate the likely trajectories of cells originating in the Firth of Forth. The model has also been used to calculate the back trajectories of cells which were present on the shore at the height of the toxic outbreak. Finally, we compare the environmental conditions in 1990, when a significant PSP outbreak occurred, with the previous year, when PSP incidence was very low. Satellite remote sensing is used to determine sea surface temperatures for 1990 and 1989, and other factors are considered which might result in the observed interannual variability.

## Method

### PSP measurement

PSP toxin was measured using the Official Methods of Analysis for the biological method to determine PSP [Association of Official Analytical Chemists (AOAC), 1984]. A total of 100–150 g of shellfish flesh was homogenized and weighed. One hundred millilitres of 0.1 M HCl were added to 100 g of homogenized shellfish and shaken for ~1 min. The pH was adjusted to between 2 and 4, and the sample placed in a boiling bath for 5 min. On cooling to room temperature, the pH was checked, the solution filtered and 1 ml was injected into 18–23 g white outbred mice. The level of toxicity of the samples was determined from the death of the animal and its weight, using published tables of the AOAC (1984).

### Dinoflagellate cyst distribution

Sediment samples were collected in the spring and autumn of 1992 in the coastal region from Aberdeen to Bridlington (Figure 1). At each station, two replicates were taken using a Day grab. Subcores of the top 5 cm of each Day grab were

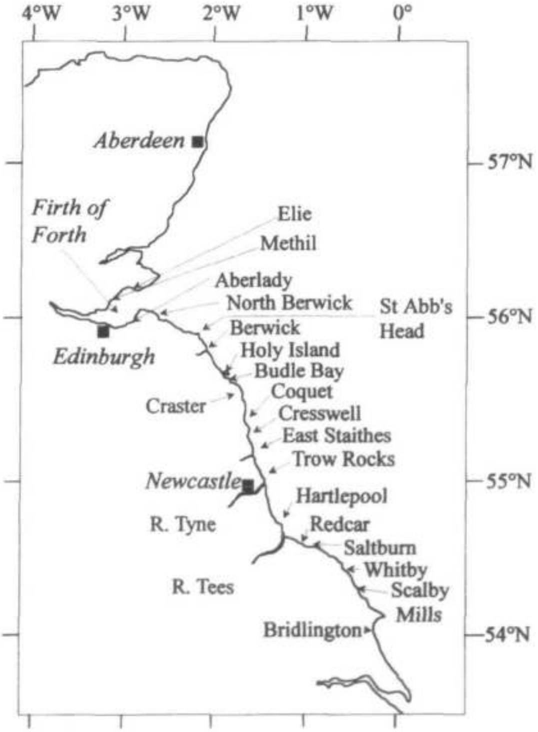

**Fig. 1.** Chart of the NE British coast showing the sites which were sampled for PSP toxin in shellfish.

placed in glass jars and stored in the dark at 5°C. The sediment was homogenized and an aliquot, usually 0.5 ml, removed; the actual volume varied slightly, depending on sediment type. The aliquot was mixed with ~10 ml of artificial sea water and sonicated for 2 min. The sediment slurry was sieved through an 80 μm mesh onto a 20 μm mesh using ~200 ml of artificial sea water. The particles remaining on the 20 μm mesh were washed into a beaker and the final volume measured. Of this final slurry, 1 ml was removed and placed in a Sedgewick Rafter Counting Chamber and examined at ×100 magnification with an Olympus BH2 microscope. The numbers of all dinoflagellate species were recorded. Dry weights were determined for each sediment sample so that cysts per millilitre could be converted to cysts per gram of dry weight.

### *Modelling particle trajectories*

The depth-averaged tide plus surge model (known as CSX) covers the domain from 46°N to 62°N and 12°W to 12°E with a grid resolution of 1/3° latitude by 1/2° longitude. This model has been run for the period 1954–1993, with inputs of gridded surface winds and atmospheric pressures, at 6 h intervals, obtained from the Norwegian Meteorological Office; model output, in the form of hourly arrays of elevation and east and north components of current, have been stored as yearly files at the Proudman Oceanographic Laboratory. Two file types, tide alone or tide plus meteorological effect (here called tide + surge), allow determination of either the tidal motion, the total motion or the residual motion. Being a depth-averaged model, no direct account can be taken of baroclinic features such as riverine-induced coastal currents. Even if baroclinic processes were included, the resolution of the model (~35 km) would preclude the simulation of such features. However, in relation to the problem in question, we do not feel that there is a need for such features to be included in this model and that given the conditions prevalent during the investigation, a depth-averaged model is sufficient to describe the predominant forces affecting dinoflagellate cell and cyst movement.

Particle trajectories were calculated using the POL oilspill model (Proctor *et al.*, 1994) with slight modification to accept the new datafiles. Although this is a comprehensive model, which includes all the factors affecting dispersion of oil, for this simulation of particle trajectories, all factors except advection by current have been omitted. Thus, only the effect of the depth-averaged current on the particle is considered. The model allows backward or forward integration to be calculated. The model also attempts to keep the particle in the water by limiting the trajectory movement to land boundaries, should the advection over the time step (1 h) take the particle onto the land. In this paper, trajectory calculations have been made for three positions (Figure 1): Berwick (55°46′N, 1°59′W), Trow Rocks (55°00′N, 1°24′W) and Whitby (54°30′N, 0°30′W). At each of these positions, significant PSP toxin values were recorded in 1990 and the model has been run with the meteorological conditions which applied in 1990. For comparison, the model was also run with 1989 data.

### *Satellite archives*

Two satellite archives were used in this study to investigate different aspects of the environmental conditions. Firstly, it is assumed that *Alexandrium* blooms originate from cysts which are in the bottom sediment; therefore, a resuspension event will be necessary to bring the cysts into the euphotic zone. The archive of the Coastal Zone Color Scanner (CZCS) was examined to find regions of high suspended sediment concentration which might indicate where active resuspension occurs. Secondly, since phytoplankton development is influenced by temperature and irradiance, the Advanced Very High Resolution Radiometer (AVHRR) was used to look for differences in sea surface temperature in bloom and non-bloom years.

The CZCS, the first satellite sensor to be optimized for biological oceanography, was launched on NASA's NIMBUS-7 satellite in 1978. It was a 1 year 'proof of concept' mission, but it continued to operate until June 1986, albeit at irregular intervals throughout its lifetime. Therefore, no CZCS images are available for 1990, when the PSP outbreak occurred. However, the total archive for the 8 years of operation is very large (NASA holds over 15 000 scenes; Yoder *et al.*, 1988) and a number of these were examined for the key period of the early spring. The CZCS sensor measured at four wavelengths and data from the sensor have been used to estimate chlorophyll concentration and suspended sediment concentrations. Algorithms to estimate chlorophyll concentration in the surface water are based on the ratio of light reflected from within the sea surface layer to the sensor at two wavelengths: 443 and 550 nm (Aiken *et al.*, 1992). Suspended solids concentrations can be determined from a single wavelength measurement, usually Band 3 (550 nm) (Gordon and Morel, 1983).

The AVHRR sensors are carried on the NOAA series of satellites and are primarily designed for operational meteorological observations. AVHRR has two broad bands in the orange–red (580–680 nm) and the near infrared (750–1000 nm), the latter enabling atmospheric correction of the visible channel. The AVHRR has a wide field of view of 2500 km, a resolution of 1.1 km × 1.1 km, but a frequent repeat cycle of up to three views per day. The sensor can be used to estimate sea surface temperature and suspended solids concentrations in coastal seas (Aiken *et al.*, 1992). A total of 46 AVHRR images were available for the period 1 April–3 May 1990 and 52 images from 1 March to 7 May 1989. About 12 images were processed in detail for each year to determine the sea surface temperature.

AVHRR thermal and visible images were acquired at the NERC Receiving Station at the University of Dundee and all data were processed in a standard way to allow comparison between images. The images were re-mapped to a Mercator projection, ensuring that they retained the original resolution of 1.1 km. Sea surface temperature was estimated from the near-infrared data, values being calculated with the daytime MCSST algorithm (McClain *et al.*, 1985).

## Results

### *PSP toxic outbreaks 1971–1992*

PSP toxin was detectable along the NE English coast in most years between 1968 and 1992, but the intensity of the outbreaks varied considerably. Figure 2 shows

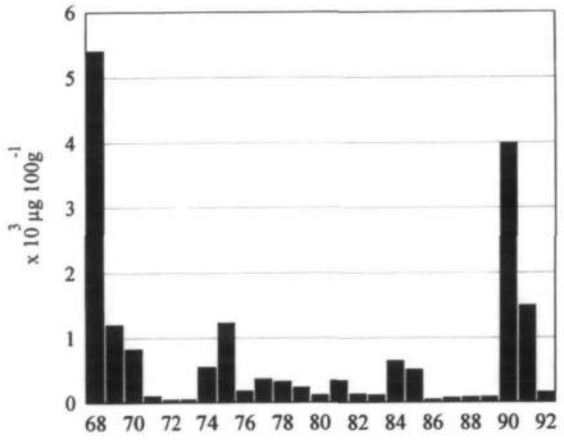

**Fig. 2.** Maximum values of PSP toxin (µg saxitoxin equivalents per 100 g shellfish) in shellfish samples collected each year between 1968 and 1992.

the maximum value for PSP toxin recorded in each year for any station between Berwick and Bridlington. This figure gives an indication of the scale of variation in the maximum toxin concentration, but the highest concentration occurred at different sites each year. After the major outbreak in 1968, elevated concentrations were recorded for the next 2 years and increased again in 1975; PSP toxin

**Table I.** Date and position of the first record of PSP in each year from 1971 to 1992; refer to Figure 1 for the position of the sample sites

| Year | First reported occurrence | Location |
|---|---|---|
| 1969 | 14 March | Holy Island |
| 1971 | 21 May | Berwick, Holy Island |
| 1972 | 6 May | Holy Island, Hartlepool |
| 1973 | 30 June | Hartlepool |
| 1974 | 11 May | Berwick |
| 1975 | 10 May | Berwick |
| 1976 | 1 May | Hartlepool |
| 1977 | 7 May | Budle Bay |
| 1978 | 14 April | Hartlepool |
| 1979 | 4 April | Cresswell |
| 1980 | 18 April | Budle Bay, Holy Island, Cresswell |
| 1981 | 9 May | Holy Island, Budle Bay |
| 1982 | 1 May | Redcar, Saltburn, Berwick, Budle Bay |
| 1983 | 10 June | Holy Island, Scalby Mills |
| 1984 | 4 May | Holy Island, Budle Bay |
| 1985 | 10 May | Budle Bay, Cresswell |
| 1986 | 23 June | Trow Rocks |
| 1987 | 19 May | Coquet, Trow Rocks, Budle Bay |
| 1988 | 6 May | Elie Beach |
| 1989 | 5 May | Elie Beach |
| 1990 | 14 May | Coquet, Cresswell, Trow Rocks, Redcar, Whitby |
| 1991 | 25 April | Berwick |
| 1992 | 27 May | Craster |

concentration remained low throughout the 1980s. However, in 1990, significant concentrations of PSP toxin were recorded at a number of monitoring sites. As a result, there was widespread closure of the shellfish fishery.

The timing of the first occurrence of PSP toxin was highly variable over the 20 year period and the geographical position of the first PSP record also changed. Table I lists the monitoring stations where PSP toxin was first recorded and the date of that record for the period 1969–1992. In many years, the earliest records are for stations in the north of the region, close to the Firth of Forth. This distribution supports the hypothesis that the source of the dinoflagellate population was close to the Forth. However, in other years, such as 1982 and 1990, PSP was widespread and appeared simultaneously at stations throughout the region. This distribution is consistent with more than one source for the dinoflagellate population.

The situation in 1989 was very different to the following year, when a significant outbreak occurred. The distributions and chronology of the outbreak in Spring 1989 and 1990 are contrasted in Figure 3a and b. In 1989, shellfish samples were collected throughout the region and tested for PSP toxin, but the number of positive tests was very small. It was absent in the earliest samples in the region from just north of the Tyne to south of the Tees estuaries at the beginning of April (Figure 3a), but was detected at a number of sites from early May. However, by mid-May, there were no more positive tests and PSP toxin was absent in shellfish samples taken through to the beginning of August.

In contrast, in 1990, PSP toxin was detected throughout the region. The toxin was absent from the earliest samples taken in April and early May (Figure 3b), but by week 20 towards the end of May, concentrations increased, with values between 40 and 80 μg saxitoxin equivalents per 100 g of shellfish tissue at sampling sites from Berwick to Whitby. The concentration of toxin which triggers closure by the authorities of the fishery is equivalent to 80 μg per 100 g. The highest concentrations (>500 μg toxin per 100 g) were measured at the beginning of June (week 21 and 22) in the region between Coquet and Trow Rocks. Concentrations remained high (80–500 μg per 100 g) over most of the region for the next 3 weeks and PSP toxin was detectable (>40 μg per 100 g) at Trow Rocks until mid-July.

### *Distribution of dinoflagellate cysts*

The predominant type of *Alexandrium* cysts found were elongated and cylindrical with rounded ends. They had thick (2–5 μm) clear walls, often with a layer of mucilage around the outer wall which accumulated detritus. The contents were clear to yellowish green in colour with a red accumulation body located in the centre of the cyst. Sizes ranged between 40 and 60 μm long, and between 25 and 35 μm wide. They closely match the description given by Anderson and Wall (1978) of *A.tamarense*.

Figure 4 shows the distribution of cysts in sediments of the North Sea sampled in spring and autumn 1992 (Lewis *et al.*, 1993). The density of *Alexandrium* cysts was between 2 and 400 whole cysts $ml^{-1}$ (3–404 whole cysts $g^{-1}$). The highest

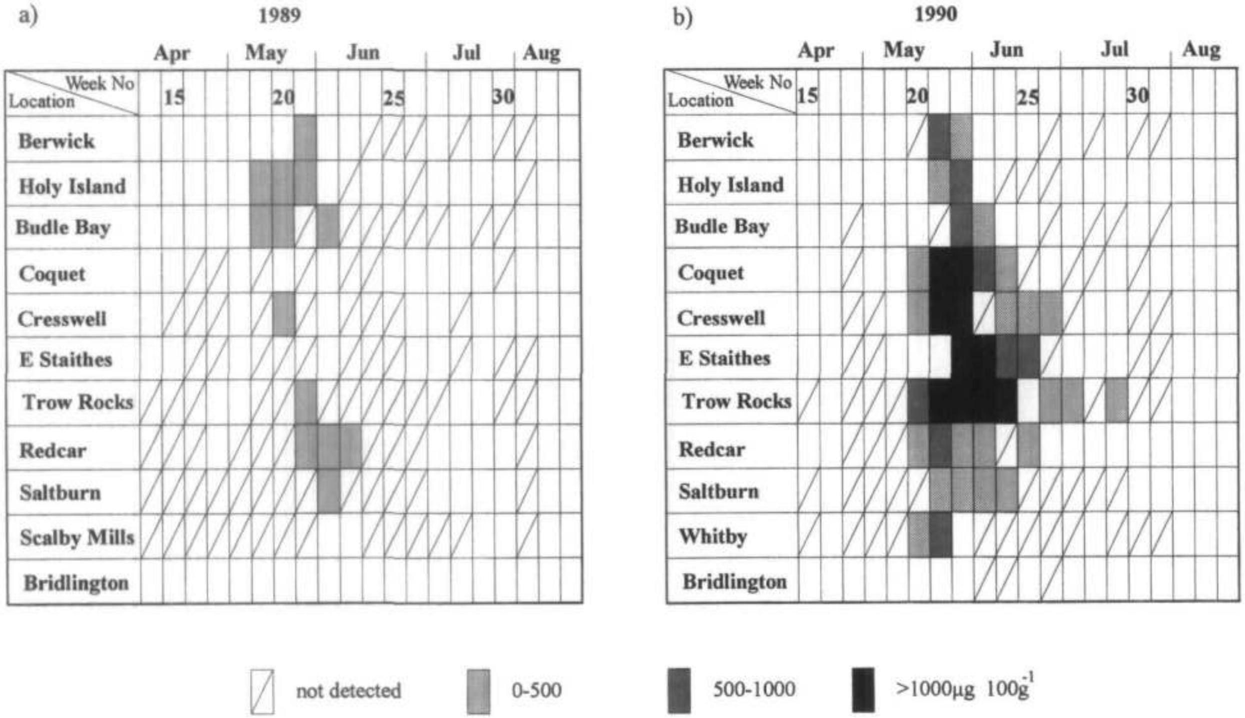

**Fig. 3.** PSP toxin concentrations in shellfish collected from Berwick (northernmost site) to Bridlington (southernmost site). (**a**) Samples collected from the beginning of April through to the beginning of August 1989. (**b**) Samples collected in 1990 for each sample site.

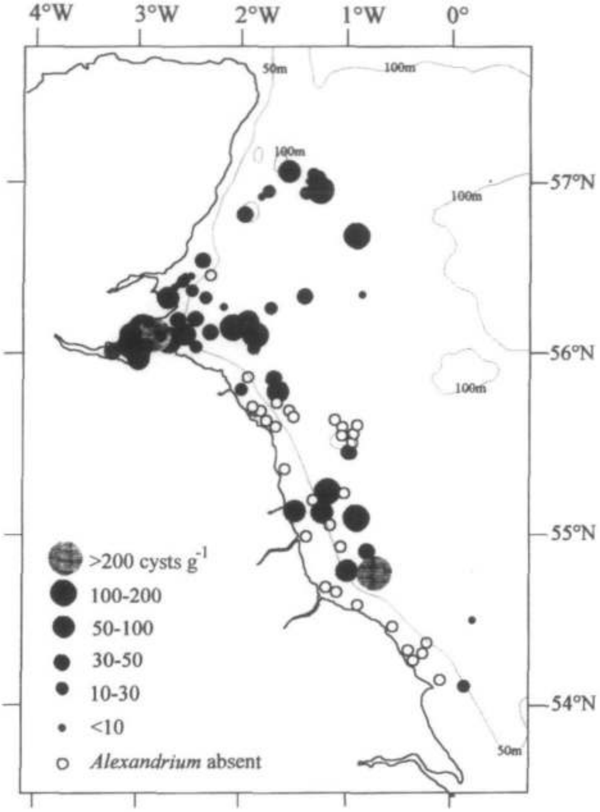

**Fig. 4.** Distribution of cysts of *A.tamarense* in 1992; the 50 and 100 m depth contours are shown.

concentration of *Alexandrium* cysts was found in the outer Firth of Forth, within the area bounded between Aberlady, Methil, Elie and North Berwick. At several stations, cyst numbers were >200 g$^{-1}$, but most sediment samples had 100–200 cysts g$^{-1}$. High numbers were found in the region to the east of the Forth and again a number of samples had 100–200 cysts g$^{-1}$. In the north of the region sampled, numbers were again elevated and sediments offshore of Aberdeen contained >50 cysts g$^{-1}$. Another region of high cyst abundance was offshore of the rivers Tyne and Tees; numbers were typically >50 cysts g$^{-1}$ and at one station off the river Tees >200 cysts g$^{-1}$ were found. Therefore, although the highest concentrations of *A.tamarense* cysts were found in the surface sediments of the Firth of Forth, their distribution was widespread and high numbers were present in other parts of the NE region.

### *Model trajectories*

The data on cyst occurrence can neither confirm nor refute the suggestion that nuisance dinoflagellate blooms originate in the Firth of Forth. Therefore, we have used an established model of North Sea circulation to investigate the possible movement of particles, which are assumed to behave in the same way as *A.tamarense* cells. A number of other assumptions are made. In these model simulations, it is assumed that *Alexandrium* cells present in the water originate from the sediment, either by resuspension of cysts or direct germination. The factors controlling excystment are not completely understood, but the process is influenced by a number of factors, including darkness, temperature and oxygen concentration (Anderson *et al.*, 1987), and a biological clock may be involved (Anderson and Keafer, 1987). To run the model, it is necessary to specify a time scale for the simulation which would include all probable periods of excystment. PSP toxin was detected in mussels on the shore from mid-May, but we do not know the exact date when excystment occurred. The development of the seasonal thermocline in the region occurs in April and, before that date, vertical mixing processes could bring cells from near-bottom water into the euphotic zone; once stratification occurs, there is little scope for dinoflagellate cysts or cells to enter the euphotic zone and begin to grow. Therefore, it is assumed that *A.tamarense* excysts before April. We also assume that excystment is unlikely before the beginning of March, when water temperatures were at a minimum. So hindcast simulations were run from week 20, in mid-May when the high PSP toxin concentrations were detected in mussels in 1990, and the simulations were hindcast back to 1 March 1990. Finally, it is assumed that cells of *A.tamarense* are neutrally buoyant and behave in the same way as a soluble component of sea water. Although *A.tamarense* is motile, we assume that in the dynamic tidal waters of the North Sea, motility is insignificant in comparison to physical mixing processes.

The aim of this experiment was to determine the trajectory which a particle (equivalent to a cell of *Alexandrium*) might have taken over a period of 80 days until it reached the shoreline on 20 May, and hence to establish the likely position of any seed bed. Three starting positions were chosen for the simulations: Berwick, Trow Rocks and Whitby. At all three sites, high PSP toxin concentrations were measured in May 1990. Figure 5 shows the back trajectories for cells which were at the shoreline on 20 May 1990. The total current (i.e. tide + surge) model was used in these calculations and the elliptical tidal excursion can be seen superimposed on the surge drift. Of the three trajectories, it is clear that only the particle which came ashore at Berwick might have originated in the Firth of Forth. If a cell from the Forth had been transported offshore to 2°W by 1 April, it could have come ashore at Berwick by 20 May. However, if excystment occurred at the beginning of March, the origin would have been offshore at ~1°W. Any *A.tamarense* cells present in the nearshore environment of Trow Rocks or Whitby in mid-May probably originated in offshore waters. These simulations do not support the hypothesis that *A.tamarense* cells responsible for the PSP toxin outbreak in 1990 originated from a single seed bed. Rather, there appears to have been a diffuse source which was some way offshore.

Although PSP toxin concentrations were very low in the previous year, a comparative exercise was carried out for 1989, and the results are shown in Figure 6. Again, over an 80 day period, there is no indication of a constant southward movement of particles along this coast from the Firth of Forth. A particle on the shoreline

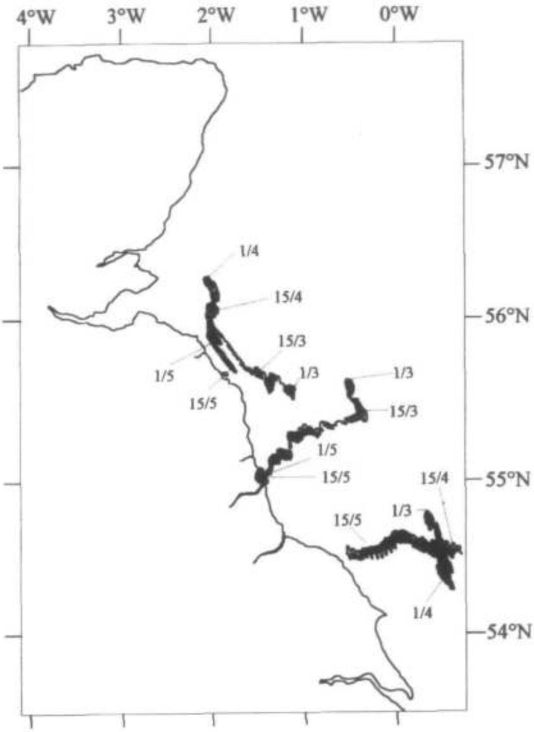

**Fig. 5.** Results of a simulation model which calculates back trajectories for notional cells of *A.tamarense* present at the shore at Berwick, Trow Rocks and Whitby on 20 May 1990.

off Whitby in mid-May had a back trajectory suggesting a general southward movement. However, a similar cell at Trow Rocks appeared to have followed a track perpendicular to the coast. The trajectory for the beginning of March 1989 appears to be stretched; this is a consequence of strong NW winds (>25 knots) on 1 March 1989. The daily mean residual circulation from the model suggests a large-scale flow down the east coast of the UK which crossed to continental Europe and moved north to the Skaggerak; this is the classic circulation pattern in the North Sea. After 1 March, winds and circulation were variable until another strong NW wind on 13 March. Daily circulation patterns clearly reflect the drift seen in the trajectories.

An alternative approach to the problem was to calculate likely trajectories for particles originating in the Firth of Forth. Trajectories were calculated at 2-weekly intervals, starting at the beginning of March. Figure 7 shows the trajectory of a cell which was in the outer Firth of Forth on 15 April 1990; another cell, with a source slightly offshore, is included for comparison. Positions within the Firth result in trajectories which cross the land because the model domain is a coarse approximation to the coastline in this area. Nevertheless, in all simulations, movement was either to the north or fairly stagnant and again does not support the hypothesis that the Firth of Forth is a seed bed of the *A.tamarense* cells which caused the PSP outbreak along the NE coast in 1990.

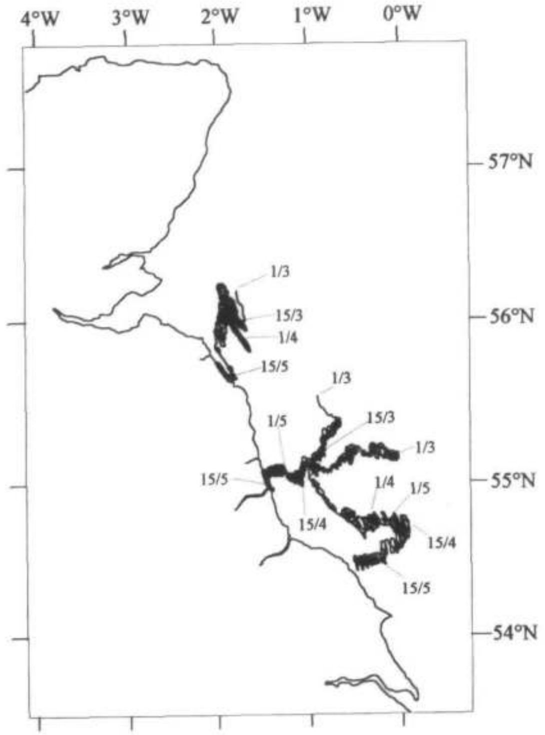

**Fig. 6.** Results of a simulation model which calculates back trajectories for notional cells of *A.tamarense* present at the shore at Berwick, Trow Rocks and Whitby on 20 May 1989.

### *Satellite images*

Images from two satellite sensors have been used in this study. The CZCS archive was of limited use because there were no significant PSP outbreaks during the operational period of the CZCS sensor. However, the images were examined to see whether there are regions, particularly within the Firth of Forth, which have high concentrations of suspended solids and where resuspension of cysts might occur. The greatest turbidity levels occurred along the Scottish coast, to the north of the Firth of Forth and in a region close to Holy Island. Within the Firth of Forth, the north shore between Methil and Elie had the highest turbidity; there was a small region offshore, close to Aberlady which also showed a localized increase in suspended solids concentrations. On the basis of these CZCS images, the regions of highest turbidity and, hence, presumably of greatest potential resuspension of bottom sediments and any dinoflagellate cysts contained therein, are the north shore of the Firth of Forth, and the Northumberland coast off Holy Island.

The second satellite sensor, the AVHRR, was more useful in this study. The AVHRR archive is much more extensive and continues up to the present day. It is less useful for quantifying suspended solids, but gives good estimates of surface

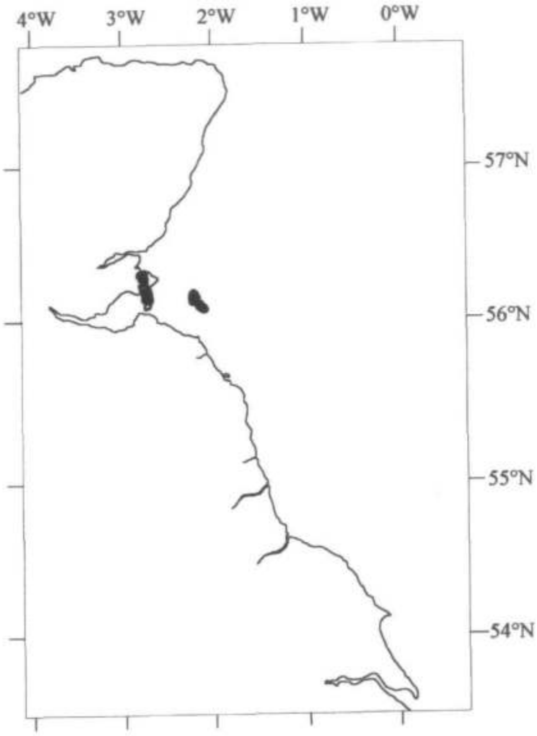

**Fig. 7.** Results of a simulation model which calculates the trajectories for notional cells of *A.tamarense* from the Firth of Forth, with a starting date of 15 April 1990.

water temperature. Since extensive AVHRR data were available for 1990, when a major PSP outbreak occurred, the data were processed to measure sea surface temperature. These data for 1990 have also been compared with 1989, when no significant PSP outbreak occurred. The aim was to investigate whether those environmental parameters which can be quantified from satellite imagery, such as water temperature and suspended solids concentration, might show variations or anomalies which were coincident with, and unique to, the time when toxic dinoflagellate blooms occurred.

AVHRR images demonstrate differences in water temperatures in the 2 years. The image for 25 April 1989 (Figure 8a) shows that the sea surface was cold, with little evidence of variability in temperature to indicate stratification of the sub-surface water. In contrast, the image for 24 April 1990 (Figure 8b) shows extensive regions of warm water offshore. There were localized patches of cold surface water, off the Northumberland coast and north of the Humber, which were largely associated with headlands, such as Flamborough Head and the Farne Islands. Therefore, in 1990 the sea surface temperature was warmer and the variability of temperature across the region indicated that stratification was developing.

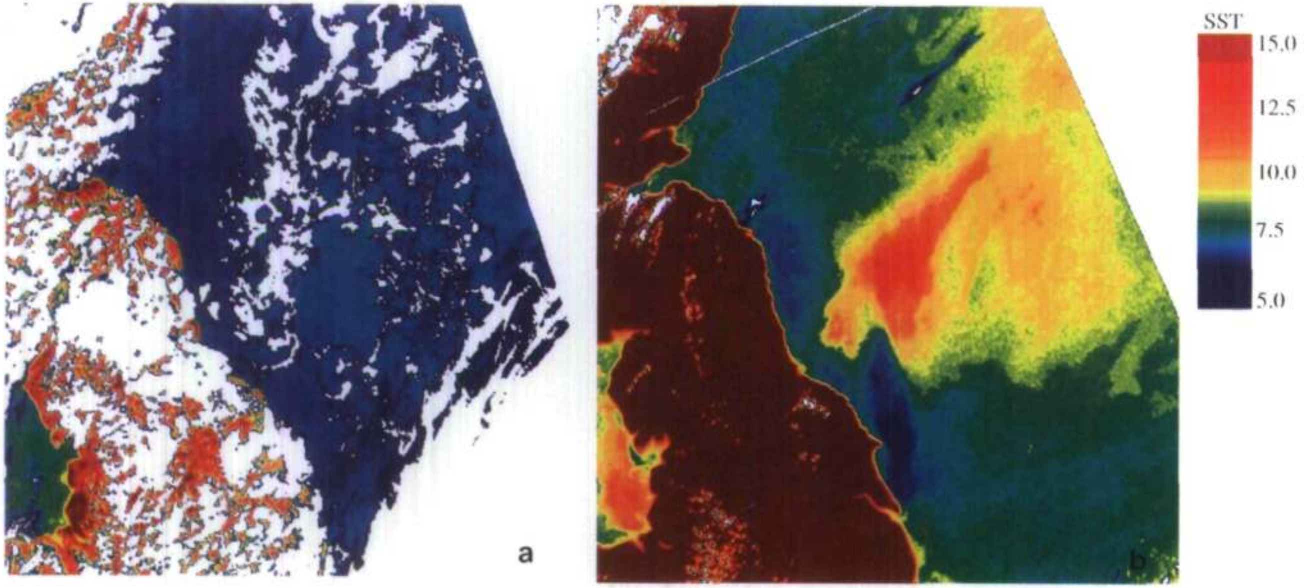

**Fig. 8.** A false colour image of data for (**a**) near-infrared image from the AVHRR sensor for 25 April 1989; (**b**) near-infrared image for 24 April 1990; white areas are regions of cloud cover.

## Discussion

The dinoflagellate genus *Alexandrium* contains a number of species which produce potent neurotoxins. Species of the genus *Alexandrium* have a worldwide distribution (Anderson *et al.*, 1994) and nuisance outbreaks are common. Within the European Union, the Shellfish Directive requires extensive monitoring to detect the presence of phytoplankton species which might produce toxins with public health implications; among these phytoplankton, *Alexandrium* species are important because of the production of toxins which cause PSP.

There is great interannual variability in the incidence of PSP toxin off the east coast of Britain. This paper has shown that, although PSP toxin has been detected in shellfish samples every year since the major outbreak of 1968, in most years, toxin levels are very low and have no impact on the shellfish industry. Yet, in other years such as 1990, the levels of toxin in shellfish flesh became dangerous and the fishery was closed. The interannual variability is unpredictable and understanding is lacking of the factors which result in PSP toxin outbreaks. As a consequence, there is no alternative to labour-intensive monitoring for PSP toxin and the presence of potentially nuisance phytoplankton species. In this paper, we have examined a number of aspects of the problem.

Firstly, we have considered the potential for the outbreak to originate from a single seed bed of dinoflagellate cysts. It is assumed that, because cysts retain viability for long periods, any outbreak will originate from excystment of cysts which have been on or in bottom sediments. The suggestion that the Firth of Forth is the source for *A.tamarense* blooms on the NE English coast has wide currency and originates in part from Robinson (1968). His description of the distribution of *A.tamarense* in CPR samples stated that '*G. tamarensis* first appeared east of the Firth of Forth in samples taken between April 19 and 21'. Wood (1968), in a chronology of the 1968 bloom, highlighted the CPR observation as the first event in the sequence which led to the PSP outbreak. The second event which Wood records is the presence of *A.tamarense* around the Farne Islands (Holy Island) in mid-May. So the idea that the Firth of Forth is the origin for the bloom seems to rely wholly on the CPR evidence. Yet, there is considerable aliasing in those data. There was no direct sampling along the NE English coast by the CPR until 29–30 May, when small numbers of cells were detected in the region from the Tyne to the Tees. No data for this region are presented for the critical times in late April and early May when *A.tamarense* might have been moving onshore. Therefore, the CPR data of Robinson (1968) do not actually exclude the possibility that there is a diffuse source of cysts which might develop and cause a PSP toxin episode.

The data on cyst distribution (Figure 4) clearly show high numbers of *A.tamarense* cysts in the sediments of the Firth of Forth. However, high numbers are also present in sediments to the north, well offshore from the Forth; indeed, numbers are high in several other areas, including well offshore of the east coast of both Scotland and England. However, there are a number of offshore sites from Berwick to Hartlepool where, although high densities of dinoflagellate cysts were found, *Alexandrium* was absent. The Firth of Forth does not appear unique; other areas could also be the source of cysts which might develop to cause a bloom. Since cyst numbers are high in the Firth of Forth, these data could support the hypothesis that this area is indeed the seed bed. Equally, the widespread distribution of cysts in the sediments offshore could also suggest that *A.tamarense* does not develop from a single source, but that excystment occurs at a number of sites and there is, therefore, a diffuse source of the *A.tamarense* bloom. It is also possible that the presence of high cyst concentrations may be a stronger indicator of deposition of material from the water column to the benthos, rather than a source to the pelagic.

The model results, driven by weather events in 1990, indicate (Figure 5) that the Firth of Forth was not the sole seed bed for the 1990 *A.tamarense* outbreak. Trow Rocks had high concentrations of PSP toxin from mid-May to mid-June and elevated values were detected through to late July (Figure 3b). Yet the back trajectories (Figure 5) show that water did not originate from the Firth of Forth, but that there was a slow transport onshore from the beginning of March until mid-May. Similarly, Whitby had positive PSP samples in mid-May, but the back trajectories (Figure 5) clearly demonstrate that there was no along-shore transport from the Firth of Forth. The only site which might be different was Berwick. It is possible that if excystment occurred at the beginning of April, *A.tamarense* cells originating offshore of the Forth might have come ashore at Berwick, but if excystment had occurred in early March, the source would have been much further south and close to the source of cells which came ashore at Trow Rocks. The model simulation for the movement of particles originating in the Firth of Forth shows very little movement from the starting point. Again, these simulations do not support the hypothesis that the Firth of Forth was the single seed bed in 1990.

Although these model simulations indicate diverse offshore sources for the *A.tamarense* bloom in 1990, the results do depend on a number of assumptions which will affect the transport of cells in the real world. In particular, the assumption of neutral density is important; if *A.tamarense* cells have rapid sinking velocities, their transport would not be simulated effectively in this model. However, we believe that the assumption of neutral density is a realistic one. One caveat is that the model is rather coarse scale and does not infer coastal current-type motion from the Firth of Forth. The question is, would a coastal current provide the mechanism for transporting dinoflagellate cells or cysts >100 km down the coast? If such a current exists (evidence from the literature is minimal and there is no indication of such a feature from the satellite images, e.g. Figure 8), the driving mechanisms would be 2-fold. As a result of the Earth's rotation, freshwater from the Firth of Forth will flow along the south side of the Firth and southwards along the coast; secondly, the inputs of freshwater along the entire Scottish coast will modify the large-scale salinity distribution of the North Sea.

Firstly, what might be the effect of freshwater outflow from the Forth? There is little information in the literature about the role this plays in coastal current formation. Craig (1972) describes the Firth of Forth as having an estuarine circulation (seawards at the surface, landwards at the bed) with most of the Firth having ambient salinity of 34.5 p.s.u., with lower salinity water (32–34 p.s.u.) leaving the Firth on its south coast and distinguishable to St Abb's Head (Figure 1). He estimates that the plume has a width of ~3 km in the Firth, with an average velocity of the outflow (based on annual total discharge) of 1.5 km $day^{-1}$ (1.7 cm $s^{-1}$). Combining the outflow from the waters of Leven, Carron, Leith and Allan and the River Almond indicates that the monthly mean discharges in 1990 were similar to those in 1989 (Hydrological Data UK, 1989, 1990), although both years show greater than average discharge in March (114 and 130 $m^3 s^{-1}$) and less than average in May (14 and 13 $m^3 s^{-1}$). The long-term annual discharge is 43 $m^3 s^{-1}$, indicating that in April and May the potential for coastal current formation was much reduced, but was greater in March. This conclusion is supported by Lindsay *et al.* (1996) who described measurements of salinity in the mouth of the Firth in 1990 and found that in March, on spring tide, salinity differences over the top 10 m were <2 p.s.u.; in May, when discharge was low, there was negligible salinity difference indicating that the waters of the Firth of Forth were well mixed at that time.

Secondly, what would be the effect of the large-scale salinity distribution? From Goedeke *et al.* (1967) and the modelling study of Jones and Howarth (1994), monthly average salinity offshore was found to change from ~33.5 to 34.4 p.s.u. over 30 km in each of the 3 months from March to May. This information, together with a knowledge of the bathymetry and the tidal currents, was input to the model of Heaps (1972), producing a density-induced coastal current of <1 cm $s^{-1}$. However, 1990 had lower than average discharge in May (Hydrological Data UK, 1990) and this would cause coastal salinities to increase towards the offshore values, again reducing the potential for a coastal current to develop. Tidal currents along the coast are quite strong (~0.5 m $s^{-1}$) and will mix any weak stratification. Finally, winds during March 1990 were often quite strong (~30 knots towards the NE) which would enhance outflow from the Firth of Forth and cause upwelling of saltier water along the NE coast. During April and May, winds were considerably weaker (10 knots) and directionally variable, with winds on occasion blowing towards the NW, opposing any southward current. Therefore, it is unlikely that there could be any significant transport of dinoflagellate cells or cysts in a coastal current.

Why did the PSP toxin appear simultaneously over such a wide geographical area? If there is no single seed bed of *A.tamarense*, excystment would have to occur at about the same time at a number of sites. Was anything different about 1990, which would explain why an *A.tamarense* bloom occurred, when there was no significant incidence of PSP toxin in the previous 4 years? A number of mechanisms might prevent the development of a bloom on the coast. If wind direction was different, excysted cells might be transported away from the shore and hence would not impact on the fishery. However, transport onshore appeared to be similar in 1989 (Figure 6), when no bloom occurred, and in 1990, when the major event occurred.

Once excystment has occurred, other factors will influence the growth of any phytoplankton species; these include the timing of stratification and irradiance in the spring. Joint and Pomroy (1993) sampled the whole of the southern North Sea, including a number of stations offshore of the NE English coast in 1989. The spring bloom occurred first in the central North Sea in late March but, off the NE English coast, chlorophyll concentrations increased at the beginning of April and were elevated until the beginning of May. There are no comparable field data for

1990. However, sea surface temperature images are useful indicators of the timing of seasonal stratification because, in this region of the North Sea, phytoplankton production increases when stratification first becomes established.

Prior to stratification, phytoplankton cells are mixed throughout the water column; in the region off the Northumberland coast, the water is much deeper than the euphotic zone (Joint and Pomroy, 1993) and phytoplankton will spend a significant time in the deep water below the compensation depth. When stratification develops, the depth of the surface mixed layer is equivalent to the euphotic depth and photosynthesis increases. The timing of stratification is also important for the development of dinoflagellates; if the population develops from benthic cysts—which excyst either in the water column or on the sea bed—there will have to be a period of vertical mixing prior to stratification, to ensure the introduction of dinoflagellates into the euphotic zone. If stratification then takes place, the vegetative dinoflagellate cells will have to compete with other phytoplankton species for available light and nutrients. Therefore, the timing of stratification is a key process in phytoplankton bloom development. Other workers have recognized the importance of water column stability; Wyatt and Saborido-Rey (1993) suggested that accumulation of PSP toxins by mussels was favoured by neap tides and periods of weak winds.

Sea surface temperature derived from AVHRR satellite images shows significant differences between 1989 and 1990. By the end of April, the surface temperature was significantly higher over much of the offshore region in 1990 (Figure 8), but there was no evidence of surface warming in the same period in 1989. Warmer surface temperatures suggest that stratification occurred earlier in 1990 than in 1989 and the spring diatom bloom may well also have been early. There were also a significantly larger number of cloud-free AVHRR images in 1990 than in 1989. With less cloud, irradiance levels would have been higher, hence favouring phytoplankton growth through greater rates of photosynthesis. However, it is not known how conditions in 1989 compare with other non-bloom years because AVHRR images have only been examined for 1989 and 1990.

The basis of interannual variability is not well understood and it is not yet possible to understand the events which result in *A.tamarense* bloom formation in some years, but not in others. *Alexandrium tamarense* and other dinoflagellate cysts are widespread in the sediments off the east coast of Scotland and NE England. We have also demonstrated that, in 1990, the source of the *A.tamarense* which caused the PSP toxin outbreak in the region was not the Firth of Forth; rather, it is likely that excystment occurred over a wide area and the *A.tamarense* cells were then transported onshore. Finally, it is clear that stratification occurred much earlier in 1990 and sea surface temperatures were higher than in 1989; either early stratification or increased irradiance may be the key to the extensive development of *A.tamarense* in 1990.

## Acknowledgements

This work is part of the research of Strategic Research Project 1 of the Plymouth Marine Laboratory, a component of the Centre for Coastal and Marine Studies of the Natural Environment Research Council. The research was partially funded by the UK Ministry of Agriculture, Fisheries and Food under contracts FC0726 (to I.J.) and FC0711 (to J.L.).

## References

Adams,J.A., Seaton,D.D., Buchanan,J.B. and Longbottom,M.R. (1968) Biological observations associated with the toxic phytoplankton bloom off the east coast. *Nature*, **220**, 24–25.

Aiken,J., Moore,G.F. and Holligan,P.M. (1992) Remote sensing of oceanic biology in relation to global climate change. *J. Phycol.*, **28**, 579–590.

Anderson,D.M. and Keafer,B.A. (1985) Dinoflagellate cyst dynamics in coastal and estuarine waters. In Anderson,D.M., White,A.W. and Baden,D.G. (eds), *Toxic Dinoflagellates*. Elsevier Scientific, NY, pp. 219–224.

Anderson,D.M. and Keafer,B.A. (1987) An endogenous annual clock in the toxic dinoflagellate *Gonyaulax tamarensis*. *Nature*, **325**, 616–617.

Anderson,D.M. and Wall,D. (1978) Potential importance of benthic cysts of *Gonyaulax tamarense* and *G. excavata* in initiating toxic dinoflagellate blooms. *J. Phycol.*, **14**, 224–234.

Anderson,D.M., Taylor,C.D. and Armbrust,E.V. (1987) The effect of darkness and anaerobiosis on dinoflagellate cyst germination. *Limnol. Oceanogr.*, **32**, 340–351.

Anderson,D.M., Kulis,D.M., Doucette,G.J., Gallagher,J.C. and Balech,E. (1994) Biogeography of toxic dinoflagellates in the genus *Alexandrium* from the northeastern United States and Canada. *Mar. Biol.*, **120**, 467–478.

Association of Official Analytical Chemists (1984) *Paralytic Shellfish Poison in Seafood, 18.086. Official Methods of Analysis of the Association of Official Analytical Chemists*, 14th edn. Williams,S. (ed.). Association of Official Analytical Chemists Inc., Arlington, VA, pp. 344–345.

Ayres,P.A. (1975) Mussel poisoning in Britain with special reference to paralytic shellfish poisoning. Review of cases reported 1814–1968. *Environ. Health*, **83**, 261–265.

Ayres,P.A. and Cullum,M. (1978) Paralytic shellfish poisoning: an account on investigations into mussel toxicity in England 1968–1977. *Fish. Res. Tech. Rep. 40.* MAFF, D.F.R., London, pp. 1–23.

Coulson,J.C., Potts,G.R., Deans,I.R. and Fraser,S.M. (1968) Mortality of shags and other sea birds caused by paralytic shellfish poison. *Nature*, **220**, 23–24.

Craig,R.E. (1972) Water movements in the Firth of Forth. *Proc. R. Soc. Edinburgh Sect. B*, **71**, 131–135.

Goedeke,E., Smed,J. and Tomezak,G. (1967) Monatskarten des Salzgehaltes der Nordsee. *Erganzungsheft zur Deutschen Hydrographischen Zeitschrift Reihe* B *(4°) 9.* Deutsche Hydrographisches Institut, Hamburg.

Gordon,H.R. and Morel,A.Y. (1983) *Remote Assessment of Ocean Colour for Interpretation of Satellite Visible Imagery. Lecture Notes on Coastal and Estuarine Studies 4.* Springer Verlag, Berlin, 114 pp.

Heaps,N.S. (1972) Estimation of density currents in the Irish Sea. *Geophys. J. R. Astron. Soc.*, **30**, 415–432.

Hydrological Data UK (1989) Institute of Hydrology, Wallingford, UK.

Hydrological Data UK (1990) Institute of Hydrology, Wallingford, UK.

Joint,I. and Pomroy,A. (1993) Phytoplankton biomass and production in the southern North Sea. *Mar. Ecol. Prog. Ser.*, **99**, 169–182.

Jones,J.E. and Howarth,M.J. (1994) Salinity models for the southern North Sea. *Cont. Shelf Res.*, **15**, 705–727.

Lewis,J., Kuenstner,S. and Higman,W. (1993) An investigation of the distribution of dinoflagellate cysts in the sediments of the north east coast of Britain. Report of contract FC0711 to Chief Scientists Group, Ministry of Agriculture Fisheries and Food, London.

Lewis,J., Higman,W. and Kuenstner,S. (1995) Occurrence of *Alexandrium* sp. cysts in sediments from the North East coast of Britain. In Lassus,P., Arzul,G., Erard,E., Gentien,P. and Marcaillou,C. (eds), *Harmful Marine Algal Blooms*. Lavoisier Intercept Ltd, Paris, pp. 175–180.

Lindsay,P., Balls,P.W. and West,J.R. (1996) Influence of tidal range and river discharge on SPM fluxes in the Forth Estuary. *Estuarine Coastal Shelf Sci.*, **42**, 63–82.

McClain,E.P., Pichel,W.G. and Walton,C.C. (1985) Comparative performance of AVHRR-based multichannel sea surface temperatures. *J. Geophys. Res.*, **90**, 11587–11601.

Proctor,R., Flather,R.A. and Elliott,A.J. (1994) Modelling tides and surface drift in the Arabian Gulf—application to the Gulf oil spill. *Cont. Shelf Res.*, **14**, 531–545.

Robinson,G.A. (1968) Distribution of *Gonyaulax tamarensis* Lebour in the western North Sea in April, May and June 1968. *Nature*, **220**, 22–23.
Wyatt,T. and Saborido-Rey,F. (1993) Biogeography and time-series analysis of British PSP records, 1968–1990. In Smayda,T.J. and Shimizu,Y. (eds), *Toxic Phytoplankton Blooms in the Sea.* Elsevier Science Publishers B.V., Amsterdam, pp. 73–78.
Wood,P.C. (1968) Dinoflagellate crop in the North Sea. *Nature*, **220**, 21.
Yoder,J.A, Esaias,W.E., Feldman,G.C. and McClain,C.R. (1988) Satellite ocean color—status report. *Oceanography*, **1**, 18–35.

*Received on October 23, 1996; accepted on March 13, 1997*