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Paralytic shellfish poisoning on the east coast of the UK in relation to seasonal density-driven circulation

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Paralytic shellfish poisoning (PSP) toxin associated with the dinoflagellate Alexandrium tamarense is found on the north-east coast of the UK in late spring/early summer. Severe outbreaks are sporadic, and knowledge of the cause and origin of the phytoplankton blooms and whether they develop from a diffuse source or from a seed population is uncertain. Recent observations of the circulation of the region demonstrate a persistent southward near-coastal flow associated with strong bottom fronts bounding a pool of cold dense bottom water isolated below the seasonal (spring/summer) thermocline. Flows extend continuously for ~500 km from the Firth of Forth to Flamborough Head before passing offshore to the Dogger Bank. These observations suggest that dinoflagellates originating from the high concentrations of A. tamarense cysts in the sediment of the Firth of Forth act to maintain a dinoflagellate population in the coastal region south to Flamborough Head, thereby maintaining the risk of PSP outbreaks.

INTRODUCTION

Successful management of the coastal environment requires a sound knowledge of both the physical processes governing the retention, dispersion and transport of contaminants, and of the life history of many marine phytoplankton species. Without this, managers cannot assess the impact of anthropogenic activity (e.g. waste disposal and sea bed disturbance) on the environment and biota, nor understand the dynamics of fish stocks and potential nuisance species in response to their environment. Significant effort [e.g. (Higman *et al.*, 1995; Joint *et al.*, 1997)] has been directed towards understanding those factors governing the occasional outbreaks of paralytic shellfish poisoning (PSP) along the east coast of the UK (Figure 1), and also into monitoring shellfish for toxins [e.g. (Ayres, 1975)]. The organism responsible for PSP is the dinoflagellate *Alexandrium tamarense*, which produces a potent neurotoxin whilst in the planktonic phase of its life cycle (Wyatt and Jenkinson, 1997). The toxin can be accumulated by shellfish and zooplankton, and transmitted up the food chain. As summarized by Joint *et al.* (Joint *et al.*, 1997), incidences of poisoning in the region are comparatively rare (10 since 1828). However, an occurrence may result in serious public health problems, such as the hospitalization of 78 people during the 1968 outbreak (Ayres and Cullem, 1978), and large-scale mortality of birds and sand eels (Adams *et al.*, 1968; Coulson *et al.*, 1968). During these outbreaks, concern for public health requires closure of the shellfish industry with attendant financial hardship and the likelihood of reduced sales following its re-opening as a consequence of adverse publicity.

Knowledge of the factors that cause the interannual variability in PSP outbreaks along the east coast of the UK is incomplete at present. If outbreaks could be predicted, management of the shellfish fishery might be improved and some reduction in the monitoring programme (to test for harmful species) may be possible. Records show that the motile stage of *A. tamarense* is present in the water column from April to July (Ayres and Cullum, 1978; Higman *et al.*, 1995). Outside this period, *A. tamarense* is present in the sediment as cysts and is largely immune to dispersion or transport. Joint *et al.* emphasize that management of the shellfishery would be aided by improved knowledge of the origin of the phytoplankton blooms and whether they develop from a diffuse source or from a seed population (Joint *et al.*, 1997). For the latter, a strategy that combines hydrodynamic modelling of prevailing conditions with monitoring offers a means by

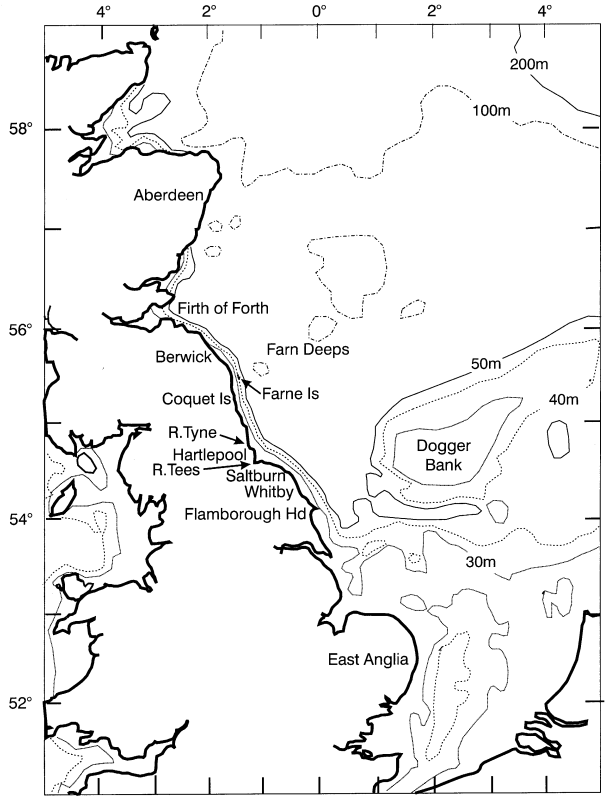


Fig. 1. Map of the east coast of the UK with topography and place names mentioned in the text.

which to predict the probability of serious harmful blooms. Joint *et al.* applied a depth-averaged tide plus surge model, with the assumption that baroclinic (density-driven) processes are unimportant (Joint *et al.*, 1997). A notable conclusion was that the source of the outbreak was not the Firth of Forth, as others had suggested [e.g. (Robinson, 1968)], but rather that the cells probably originated from a wide area and were transported onshore through the action of wind-induced circulation. However, recent work (Brown *et al.*, 1999) and new data reported here for the first time demonstrate the existence of a strong and persistent seasonal baroclinic coastal southward transport. The flow is driven by bottom density fronts that fringe the dense pool of cold winter water formed in the central North Sea following the onset of the seasonal heating cycle. We consider the role of this circulation in providing a mechanism to transport *A. tamarense* cells southwards from the Firth of Forth, where concentrations are known to be greatest (Lewis *et al.*, 1993), to cause the sporadic incidences of serious toxic outbreaks.

PHYSICAL BACKGROUND OF THE REGION

Bordering the coastline and extending ~300 km between Flamborough Head and the Firth of Forth is a narrow (~10 km) and shallow (<30 m) coastal strip (Figure 1). To the east, the topography shelves to >70 m, reaching a maximum of 113 m in the Farn Deeps. Inshore, peak tidal velocities are ~0.6 m s^{-1}, falling to typically 0.45 m s^{-1} in the deeper region (Gmitrowicz and Brown, 1993). Offshore, the combination of deep water and weaker tides means that the water column stratifies during the spring and summer heating season when there is insufficient tidally generated turbulent kinetic energy to maintain vertical mixing against the input of surface buoyancy (Simpson and Hunter, 1974). The onset of stratification occurs in April/May and isolates a pool of cold dense winter water below the thermocline (Harding and Nichols, 1987; Brown *et al.*, 1999). This body of water is separated from the warmer tidally mixed coastal waters by horizontal bottom fronts. The frontal zone is centred approximately along the line of the 50 m contour and extends from the Firth of Forth to Flamborough Head, where it passes offshore toward the Dogger Bank. The mean annual freshwater discharge along this coastal strip is 285 m^3 s^{-1}, and is maximal in winter. In spring, it can represent a significant localized buoyancy acting to bolster thermal stratification during its inception in the coastal region. The timing of thermal stratification and frontal set-up varies annually by up to a month, dependent on the degree of surface warming, wind mixing and riverine discharge.

Previous descriptions of the mean residual circulation in the central North Sea indicate a broad and weak (<0.04 m s^{-1}) anticlockwise flow that passes down the east coast of the UK before extending eastward from the coastline of East Anglia [e.g. (Lee and Ramster, 1981; Backhaus and Reimer, 1983; Davies, 1983; Prandle, 1984; Durance, 1989)]. On time scales of weeks, flow is depicted as variable and wind driven. However, such schema neglect the role of seasonal stratification and the density-driven component of the circulation associated with frontal zones.

Dynamically, it is expected that relatively narrow jet-like circulations are associated with bottom-dominant fronts (Garrett and Loder, 1981). It is only recently that observations have provided convincing direct evidence of such flows on the European Shelf. A recent series of papers describe measurements in the Irish Sea, Celtic Sea and Hebridean Shelf (Hill *et al.*, 1994, 1997a,b; Horsburgh *et al.*, 1998, 2000), showing fast (>0.15 m s^{-1}), narrow (10–20 km wide) jets above bottom fronts bordering cold (or salty) dense pools of bottom water trapped in deep basins during summer months. These 'cold pool jets' flow in a cyclonic sense (cold pool waters to the left in the northern hemisphere), and can extend continuously for hundreds of kilometres. It is important to note that it is the near-bed density front that is dynamically significant, and that in many tidal mixing systems surface and bottom fronts do not coincide—there may even be a bottom front without an attendant surface front. In this respect, infrared satellite imagery is not a reliable means of identifying these flows.

DENSITY-DRIVEN CIRCULATION IN THE NORTH SEA

Observational evidence for a density-driven near-coastal flow along the east coast of the UK was described by Gmitrowicz and Brown (Gmitrowicz and Brown, 1993). Data from an array of 27 current meters moored at 12 locations offshore between the River Tyne and Whitby (Figure 1) in the summer of 1988 demonstrated a persistent south-eastward along-shore flow at the surface and mid-depth. Results from correlation models and a multivariate spectral model showed that wind played a secondary role to baroclinic (density) processes in forcing the mean flow. Surface non-wind-driven mean flows of up to 0.08 m s^{-1} were recorded in the vicinity of the strongest bottom temperature gradients. A contemporaneous acoustic Doppler current profiler (ADCP) survey during 1 week in August was undertaken along a line normal to the coast and close to the mooring array (Lwiza *et al.*, 1991), and indicated a southward non-tidal flow of up to 0.08 m s^{-1} where the isotherms began to intersect the bed.

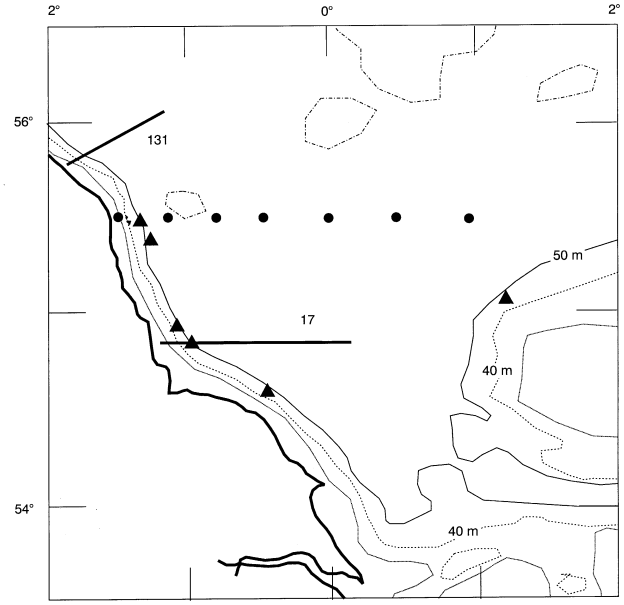


Fig. 2. The locations of Scanfish sections (solid lines) shown in Figures 3 and 4, deployment positions of the satellite-tracked drifters (▲) and the station positions for the CTD data (●) presented in Figure 6.

A limited set of observations in the central North Sea during June and July 1996 (Brown *et al.*, 1999), using towed undulating CTD and satellite-tracked drifting buoys, established the existence of a strong and persistent jet-like circulation associated with the seasonal bottom fronts. This circulation extended south from the Farne Islands to Flamborough Head and then eastward to the Dogger Bank. The new observations presented here, taken from the RV 'Corystes' during two periods in 1997 (18–30 July and 22 August–2 September), constitute a more detailed survey of the coast from the Firth of Forth to Flamborough Head (Figure 2) and confirm the circulation pattern proposed. Between the cruise periods, the flow field was measured directly using satellite-tracked Argos drifters, with holey sock drogues 5.5 m high and 1.5 m diameter, centred at 30 m depth. Positional fixes during the deployments were obtained at a rate of 4–12 day^{-1} with a standard deviation in the position estimate of between 150 and 1000 m.

Measurements of temperature and salinity were made using a Scanfish towed undulating CTD system (Brown *et al.*, 1996; Fernand, 1999). This computer-controlled vehicle, towed at typically 3.0–4.5 m s^{-1}, enables profiling from within 4 m of the surface to within 5 m of the sea bed at a separation equivalent to conventional CTD profiles of ~100–500 m, the latter largely dependent on bottom depth. The vehicle was fitted with a Falmouth Scientific, Inc. Integrated CTD. Calibration of the temperature and salinity data was performed as described in Brown *et al.* (Brown *et al.*, 1999) and Fernand (Fernand, 1999). All salinities quoted hereafter were determined using the practical salinity scale (UNESCO, 1981).

Figures 3 and 4 show temperature, salinity, density and geostrophic velocity from two of the Scanfish sections normal to the north-east coast of England. Section 17 (Figure 3), taken on 21 July 1997, shows a narrow coastal zone with a comparatively weak thermocline and bounded to the east by a series of strong temperature fronts (Figure 3A), which intersect the sea bed. Here, salinity (Figure 3B) contributes relatively weakly to the structure of the water column and consequently the density field closely follows that of temperature. Offshore, there is a pool of dense cold winter water isolated below the strong thermocline.

Computed geostrophic velocities normal to the section (Figure 3D) were calculated relative to an assumed level of no motion at the sea bed. Only velocity components normal to the section can be computed, so the maximum possible geostrophic flow is underestimated if sections cross density gradients obliquely. In the raw data, the

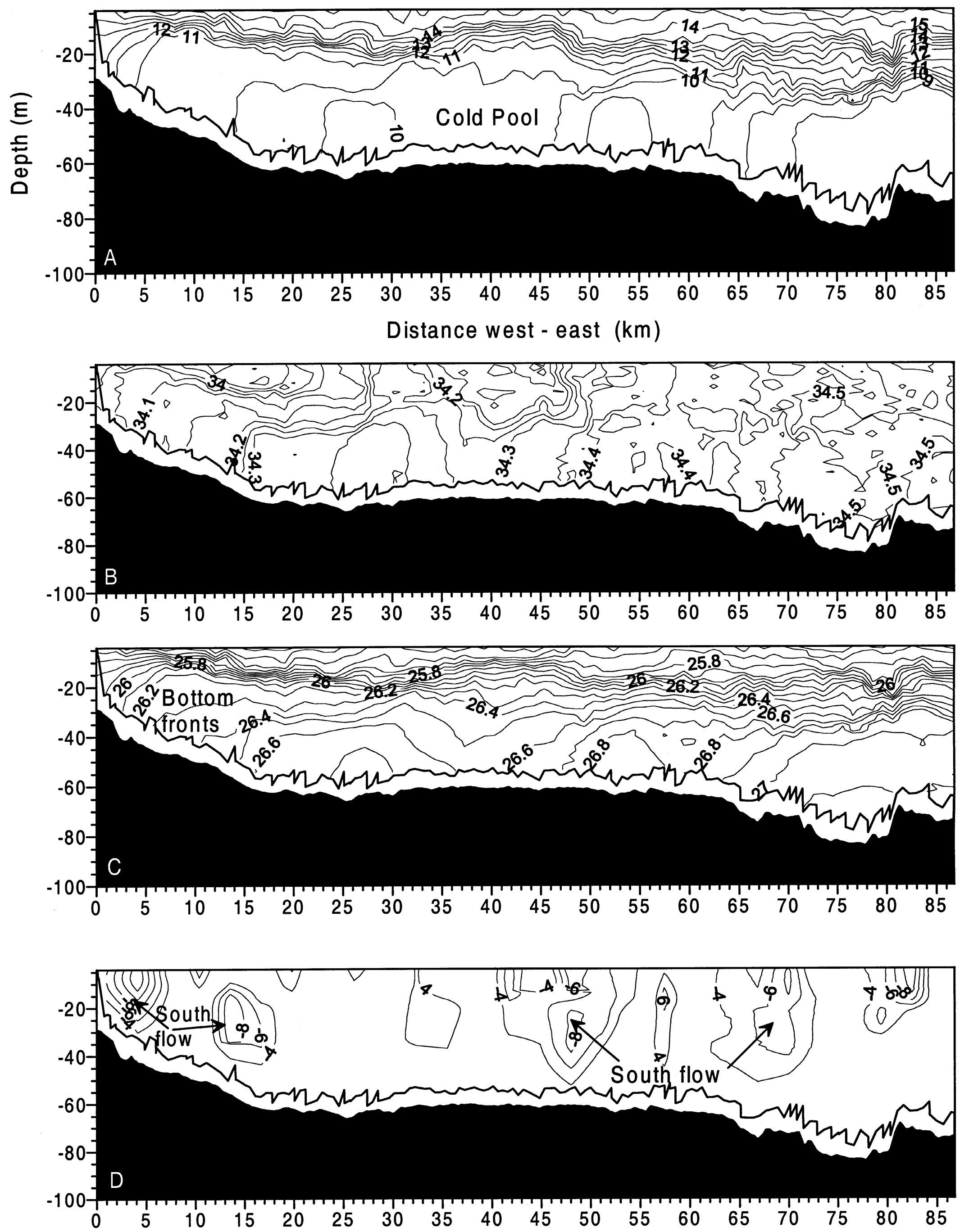


Fig. 3. Scanfish section (17; 21 July 1997) showing (**A**) temperature (°C), (**B**) salinity, (**C**) density σ_t (kg m^{-3}) and (**D**) geostrophic velocity V_g (cm s^{-1}) relative to a reference level at the deepest common depth between adjacent CTD profiles. Positive velocities indicate northward flow and negative velocities are southward flow. The profile of the sea bed (solid) is derived from the ship's echo sounder.

horizontal distance between equivalent points in successive 'V'-shaped profiles is 200–800 m. The data shown in Figure 3A–C were gridded to a resolution of 1 km in the horizontal and 1 m in the vertical using a minimum curvature scheme, and then contoured. At this resolution, small-scale perturbations were present on the pycnocline (Figure 3C), probably resulting from high-frequency processes (e.g. internal waves) and thus not likely to be dynamically significant at sub-tidal and sub-inertial time scales. In order to aid the visualization of the geostrophic velocity field, data were gridded at 3 km horizontal resolution and only velocities >0.04 m s^{-1} are presented in Figure 3D. The results show cores of southerly flowing jets (>0.08 m s^{-1}) coincident with the bottom fronts.

The more northerly section (Section 131), occupied on 26 August 1997, shows a similar structure (Figure 4) with a strong near-surface thermocline (Figure 4A) and bottom density fronts (Figure 4C) intersecting the shallowing sea bed and marking the boundary of a deep pool of dense water. Computed geostrophic velocities again show

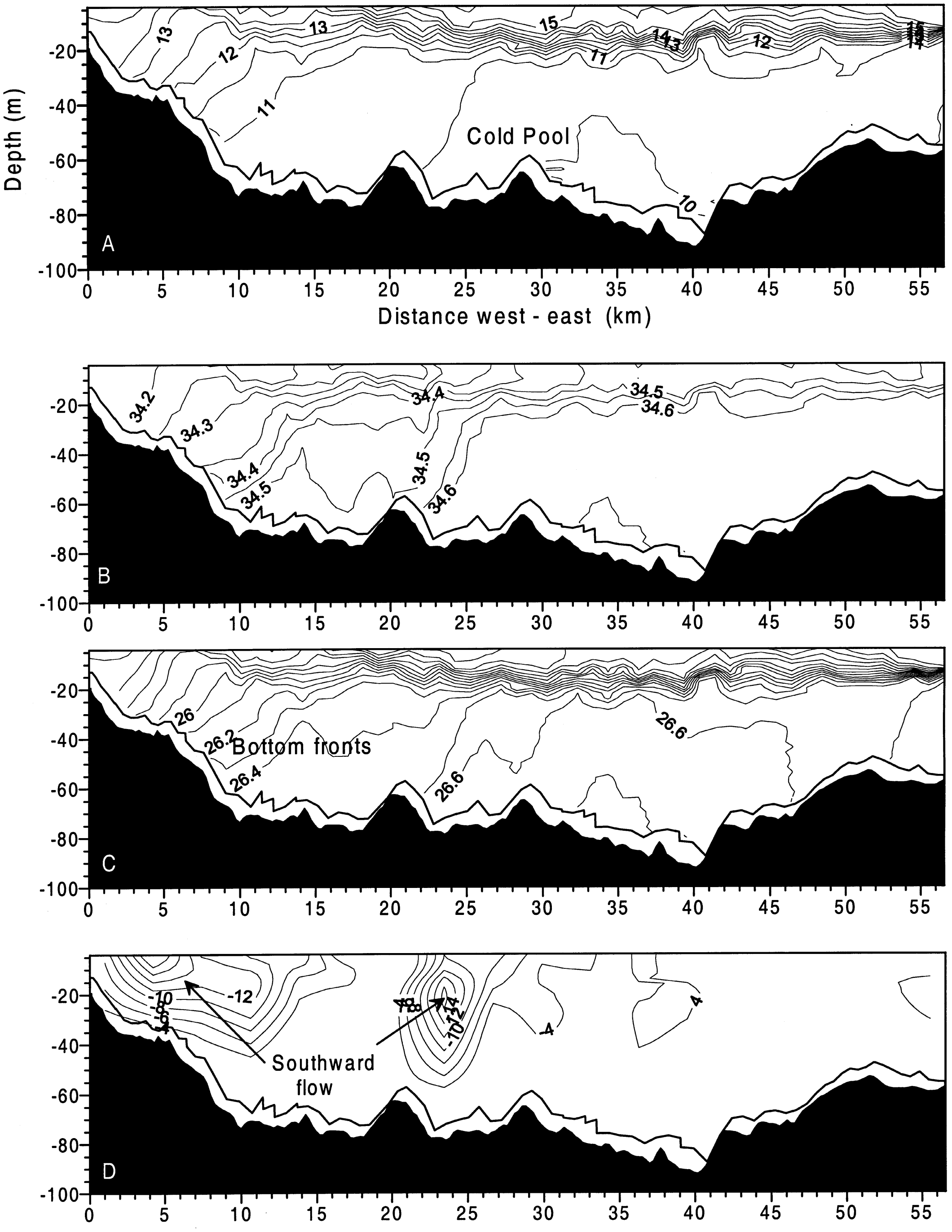


Fig. 4. Scanfish section (131; 25 August 1997) showing (**A**) temperature (°C), (**B**) salinity, (**C**) density σ_t (kg m^{-3}) and (**D**) geostrophic velocity V_g (cm s^{-1}) relative to a reference level at the deepest common depth between adjacent CTD profiles. Positive velocities indicate northward flow and negative velocities are southward flow.

southerly flowing jets associated with the bottom fronts with velocities >0.10 m s^{-1}. Here, closer to the Firth of Forth, the influence of salinity (Figure 4B) is more pronounced, contributing ~36% to the horizontal density differences that drive the inshore flow, as opposed to 25% in the more southerly section (Figure 3). In both sections, a second comparatively narrow offshore salinity front, with associated jet, contributes ~50% to the density gradient.

Five satellite-tracked drifters were deployed in the vicinity of the 50 m contour between the Farne Islands and Whitby (Figure 2). In Figure 5, drifter trajectories are shown by the coloured lines; also shown (continuous lines) are contours of density (σ_t) at the sea bed and the solid arrows depict calculated geostrophic velocities at the core of flow associated with the bottom fronts.

Three of the trajectories were of comparatively short duration (~9 days) in order to accommodate concerns that they might interfere with inshore salmon nets. Four of the instruments moved southwards parallel to the coast at mean velocities of between 0.04 and 0.08 m s^{-1}. The most southern of these (duration 30 days) travelled south to the boundary between the stratified and mixed water near Flamborough Head. The fifth drifter initially followed the bathymetry, but then passed offshore, reaching the north-west corner of the Dogger Bank, travelling 225 km in 42 days at a mean velocity of 0.06 m s^{-1}. A further drifter, deployed almost at the end position of the latter, demonstrated the continuity of flow eastward. This pattern corresponds to that of two drifters deployed above the 50 m contour at ~54°51′N 01°06′W in late June 1996 and drogued at 23.5 m depth (Brown *et al.*, 1999). These drifters moved parallel to the bathymetry at mean velocities of 0.07 and 0.06 m s^{-1}. It is evident in Figure 5 that drifter tracks have a tendency to follow the spatial structure of density (rather than bathymetry). That density should act as a contour map for residual flow is a strong indication that the flow is responding to baroclinic forcing. The direct influence of the wind was discounted as a forcing mechanism by performing correlations between

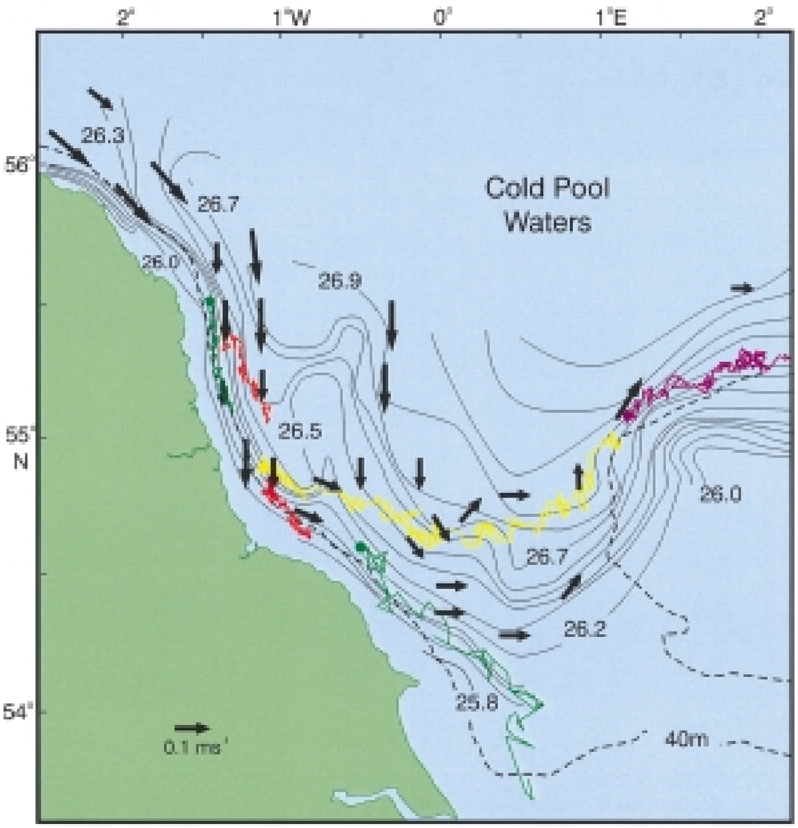


Fig. 5. Contours of bottom density (σ_t) derived from a series of Scanfish sections undertaken during 1997 (predominantly 18–30 July, but those north of the Farne Islands on 25–26 August). Overlain are the trajectories of six satellite-tracked drifters drogued at 30.0 m. The start position of each track is at the north-west (see Figure 2). The solid arrows represent the velocity of the core of flow associated with the bottom fronts and derived from geostrophic estimates. Only velocity components normal to the sections can be computed, so the maximum possible geostrophic flow is underestimated if sections cross density gradients obliquely.

the mean daily fluctuations in drifter and wind velocity components, as in previous work [e.g. (Horsburgh *et al*., 1998)]. Statistically significant correlations of both velocity components were not obtained. Wind forcing was also ruled out by the basic differences in the shape of drifter trajectories over a horizontal distance where the wind field would not be expected to vary.

SEASONAL DEVELOPMENT OF THE BAROCLINIC CIRCULATION

The observations presented above demonstrate the existence of a well-defined and persistent coastal flow extending from the Firth of Forth to Flamborough Head. The flow is associated with seasonal bottom fronts that fringe the margins of the pool of cold winter water in the central North Sea. The observations in 1996 and 1997 were undertaken at the height of the heating season in order to define the mature density and flow fields. However, PSP toxin in shellfish is generally detected between early May and late June (Joint *et al.*, 1997), requiring that *A.tamarense* cells be present in the water column from mid-April at the latest. Data that describe the formative period of stratification (April–June) are few. Additionally, significant interannual variability in the timing of the onset and strength of stratification is to be expected, largely dependent on the wind strength (mixing of the water column), cloud cover (heating) and river discharge. The episodic nature of the latter means that contribution to flow variability is also likely on time scales of weeks.

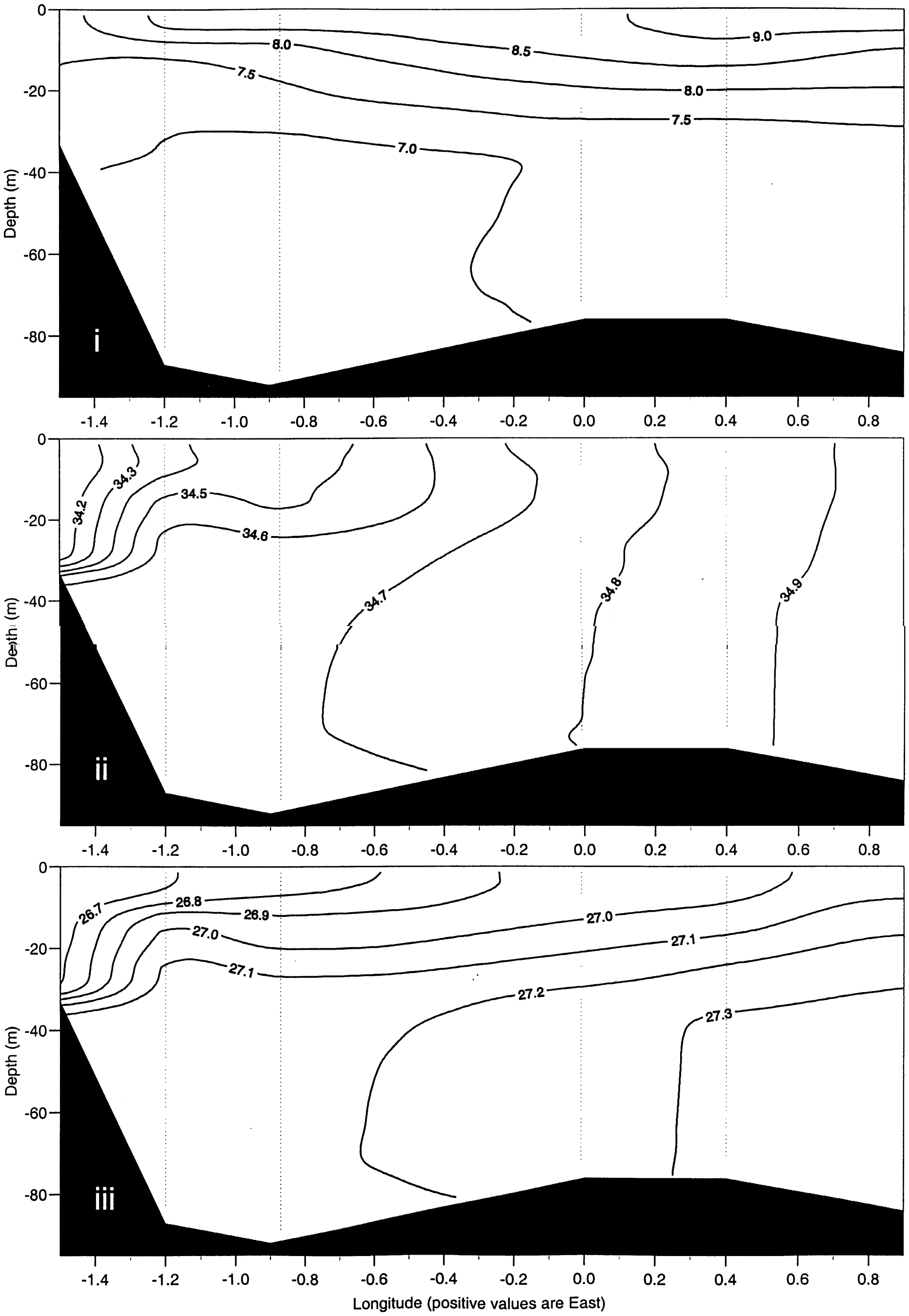
The most spatially complete seasonal survey of temperature was that reported by Harding and Nichols (Harding and Nichols, 1987) and Brown *et al.* (Brown *et al.*, 1997). These data, obtained in 1976, showed that thermal stratification was established by mid-May, with surface to bottom temperature differences >2°C. The transition from coastal mixed to offshore stratified waters was centred over the 50 m contour and extended from the northern limit of the survey region off Berwick (~56°N) to the River Tees, before passing eastwards towards the Dogger Bank. By late May, surface to bottom temperature differences exceeded 5°C with a well-defined coastal front. Inshore surface waters were ~0.5 fresher than those offshore, enhancing density gradients.

The region lies within the area covered by the Natural Environmental Research Council (NERC) North Sea project in 1988–89 [e.g. (Howarth *et al.*, 1993)], which included a repeated line of CTD stations along latitude 55°30′N. The observations show that on 7 April 1989, the water column was vertically mixed, but by 5 May temperature stratification of 1.5°C had formed, which along with the influence of coastal run-off produced a distinct bottom front intersecting the sea bed near the 40 m contour (Figure 6a). By 3 June, thermal stratification was stronger (>3.0°C), with a weaker salinity component, but pronounced bottom fronts characteristic of full summer stratification (Figure 6b) were seen. The data from 1976 and 1989 provide evidence that by early May seasonal heating of the water column, augmented by coastal discharge, is sufficient to generate significant bottom fronts. Dynamically, even at this formative stage, baroclinic southward flow would be expected. Calculated geostrophic currents would be weaker than those in Figures 3D and 4D for two reasons: the density gradients are weaker and the spacing of the CTD stations is of the order of 30 km, much greater than the resolution of the Scanfish data. Geostrophic calculations based on the data would not adequately represent the flow.

IMPLICATIONS OF THE FLOW FOR PSP

Typical mean speeds of the baroclinic flow between the Firth of Forth and Flamborough Head exceed 0.06 m s^{-1} (>5 km day^{-1}) and those at the core exceed 0.15 m s^{-1} (>13 km day^{-1}). Given that *A. tamarense* cells are present within the water column between April (excystment) and July (encystment), it is reasonable to enquire whether the pronounced circulation plays a role in the dynamics of PSP outbreaks in the region. Surveys of surface sediment in spring and autumn 1992 (Higman *et al.*, 1995; Lewis *et al.*, 1995; Joint *et al.*, 1997) showed that concentrations of *A.tamarense* cysts in sediment were greatest in the outer Firth of Forth and offshore of Aberdeen. A significantly smaller patch was found offshore of the rivers Tyne and Tees. In general, the highest cyst populations were associated with finer grained sediment, although curiously none were found in the Farn Deeps. However, between Berwick and Hartlepool, relatively coarse sediments contained *A. tamarense* cysts.

Records collected at coastal monitoring stations from 1969 to 1992 (Higman *et al.*, 1995; Joint *et al.*, 1997) indicate that the earliest occurrence of PSP toxin was generally in the northern part of the region, particularly between Berwick and Hartlepool. However, the toxin only occasionally appears first in the Firth of Forth, and on three occasions (1982, 1983 and 1990) the toxin occurred in the south of the region at the same time as the north. Joint *et al.* concentrate on a comparison between 1989, when very little toxin was recorded, and the outbreak of 1990 (Joint *et al.*, 1997). During 1989, PSP was first recorded on the north coast of the Firth of Forth on 5 May and then successively down the coast to Saltburn at the end of May. In 1990, the first recorded occurrences were

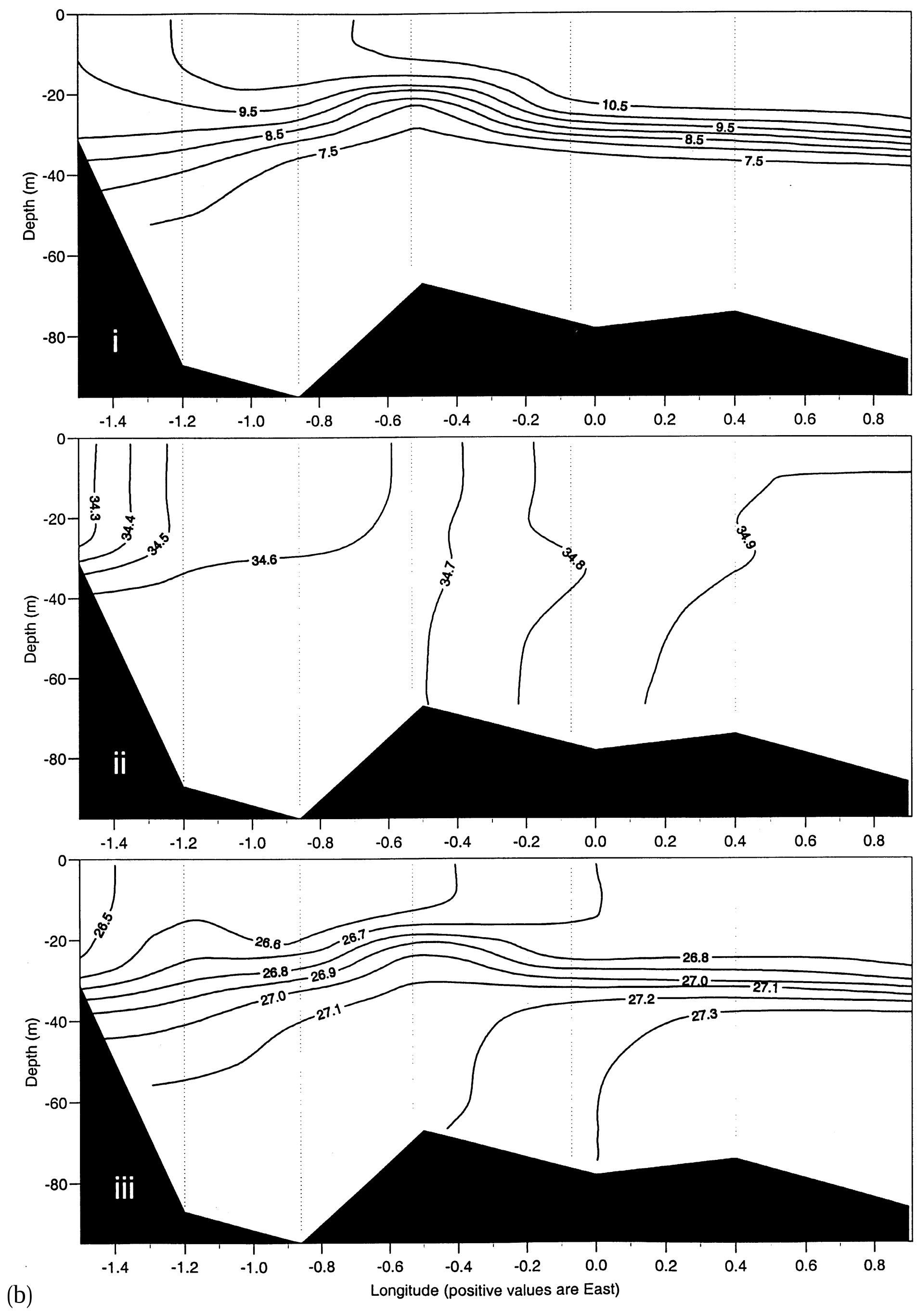


(a)

Fig. 6. Temperature (°C) (**i**), salinity (**ii**) and density (σ_t; kg m^{-3}) (**iii**) data from NERC CTD surveys along latitude 55°30′N. Station positions (● in Figure 2) are represented by vertical dashed lines and vertical margins of the plots. (**a**) 5 May 1989. The structure of near-coastal bottom fronts is largely determined by salinity. (**b**) 3 June 1989. Following seasonal heating, the structure of near-coastal bottom fronts is largely determined by temperature.

on 14 May at five sites stretching from Coquet to Whitby. The peak of the outbreak was centred in this region from mid-May to late June.

The North Sea Project data (Howarth *et al.*, 1993) show that in 1989 stratification and bottom fronts had begun to form in early May. Data for 1990 are few, but infrared satellite imagery for April and May 1989 and 1990 (Joint and Aiken, 1994) indicated that in late April/early May 1990 surface warming of the water column was more advanced than in 1989. This is



supported by limited CTD data, available from the International Council for the Exploration of the Sea (ICES) database, and weekly surface temperature distributions of the North Sea, published by the Bundesamt für Seeschiffahrt und Hydrographie (BSH) [e.g. (Loewe, 1996)]. Data suggest that surface temperatures in the North Sea, at ~55°30′N 1°33′W, were warmer by 1°C in 1990 compared to 1989.

DISCUSSION

Even if stratification and attendant bottom fronts were stronger in the early part of the season during 1990, southward coastal transport is expected to be relatively weak (<5 km day^{-1}). This, combined with the knowledge that PSP was detected simultaneously at a number of locations along the coast, argues against the Firth of Forth being the immediate source for the 1990 outbreak. There are also difficulties associated with the suggestion that the source of cells is offshore. No cysts have been recorded in the sediments of the deeper offshore waters of the region (Higman *et al.*, 1995; Lewis *et al.*, 1995; Joint *et al.*, 1997), even in the Farn Deeps, an apparently favourable site given the fine sediment and low tidal energy conducive to settling of material. The 'trigger' for excystment of *A.tamarense* is uncertain, but may be in response to a signal of an endogenous circannual clock (Anderson and Keafer, 1987; Wyatt and Jenkinson, 1997), perhaps combined with increasing water temperature (Anderson and Morel, 1979), bottom disturbance (Joint *et al.*, 1997) and increased light levels (Anderson *et al.*, 1987). An environmental cue for excystment in March in water depths exceeding 60 m is unlikely. Warming of surface waters generally begins in April and near-bed temperatures in stratified regions increase only very slowly (Elliott *et al.*, 1991; Brown *et al.*, 1999). Significant disturbance of sediment by storm events in such depths is improbable and light levels are low.

An endogenous circannual clock remains a candidate, but there would be a small window of opportunity before thermal stratification isolated the deep offshore waters from the coastal zone. Furthermore, the strong stratification and jet-like coastal flow during encystment in June and July present difficulties for the maintenance of a seed population because of the advection of *A. tamarense* from the coastal zone to deeper offshore waters. During the toxic bloom of 1968, Robinson reported that *A. tamarense* cells were detected within 40 km of the coast (Robinson, 1968). Cysts in the nearshore (<30 m depth) sediments are most likely to provide the innoculum for the spring/summer bloom. Here, the water column stratifies intermittently and any or all of the above environmental cues could trigger excystment.

Given that cysts may remain viable for at least 10 years (Wyatt and Jenkinson, 1997), the role of advection in the maintenance of blooms on the east coast must be considered. Neglecting the question of cyst origin, there appear to be sufficient numbers in the near-coastal sediments to provide the seed population for significant blooms. However, once in the plankton, *A. tamarense* will be advected southward with the mean flow. At typical speeds of 0.07 m s^{-1}, the transit time between the Farne Islands and Flamborough Head (~210 km) is 33 days. Without continual replenishment, the mean flow field would prevent maintenance of the population. We have discounted the possibility that the Firth of Forth provides the immediate source of *A. tamarense* for toxic blooms. Nevertheless, it is conceivable that each year a significant quantity of *A. tamarense* from the Firth is carried in the coastal flow where subsequent encystment maintains the population of cysts in the sediments along the northeast coast of England. Advection may also explain why cysts are found in the comparatively coarse sediments of the northeast coast (Lewis *et al.*, 1995).

Notably, there are no recorded instances of PSP south of Flamborough Head despite an extensive shellfishery there. The jet-like circulation described passes eastward at the latitude of Whitby before skirting the north-west corner of the Dogger Bank (see Figure 5) so there is no significant transport towards the south of Flamborough Head. It might, therefore, be expected that cysts would be found in the offshore sediments along the transport path and in the vicinity of the Dogger Bank. To date, there have been no sediment surveys in these areas and this represents a useful future study opportunity. There remains no definitive explanation for the significant outbreak of PSP poisoning in 1990 compared to other years, although limited observational evidence suggests that in 1990 there was a period of calm weather in mid-May when stratification developed comparatively rapidly. Wyatt and Sabrido-Rey suggest that a rapid increase in stratification is conducive to the growth of *A. tamarense*, which may in turn promote the production of toxin (Wyatt and Saborido-Rey, 1993).

Our observations suggest that whilst *A. tamarense* cysts continue to be present in large numbers in the sediment of the Firth of Forth, the coastal region south to Flamborough Head is likely to remain at risk from outbreaks of PSP. It is improbable that the offshore sediments act as a significant seedbed for blooms, although periods of easterly wind followed by calm conditions may act to concentrate motile cells near the shore and therefore promote toxic blooms. To understand the factors that determine the movement and concentration of cells requires numerical models that replicate the appropriate physics at a horizontal resolution of 1–2 km. Such three-dimensional baroclinic models now exist [e.g. (Proctor and James, 1996; Horsburgh, 1999)] and their predictive abilities are being tested against data such as those described here. However, before they can fully realize their potential as management tools, a fuller understanding of the factors that promote algal blooms is required.

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