

# The spring bloom and its impact on benthic mineralisation rates in western Irish Sea sediments

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**ABSTRACT:** The impact of the spring bloom on benthic remineralisation rates was studied in offshore waters of the western Irish Sea during 1998. Initiation of the spring bloom coincided with the onset of thermal stratification at the end of April. Peak chlorophyll biomass ( $6.48 \text{ mg chl m}^{-3}$ ) and algal standing stock ( $145.0 \text{ mg chl m}^{-2}$ ) were measured on May 11, and the bloom lasted approximately 1 mo. Sediment oxygen uptake increased to  $1658 \text{ } \mu\text{mol m}^{-2} \text{ h}^{-1}$  for a short period in early May, which was followed by increased denitrification (up to  $48 \text{ } \mu\text{mol N m}^{-2} \text{ h}^{-1}$ ) in late May and early July. Subsequently sulphate reduction increased (up to  $83 \text{ } \mu\text{mol SO}_4^{2-} \text{ m}^{-2} \text{ h}^{-1}$ ) in early July. Efflux of nitrate remained low but constant ( $10 \text{ } \mu\text{mol m}^{-2} \text{ h}^{-1}$ ) throughout the study, accounting for 27% of ammonified organic N, with the remaining 63% being denitrified. Sediment depth profiles of chlorophyll and phaeopigment showed deep (>30 cm) mixing of phytodetritus into the sediment in early July, which may explain the high rates of sulphate reduction measured at this time. Evidence of a large phytodetrital flux to the benthos during spring 1998 was limited. Deepening of chlorophyll isopleths suggested sinking of algae in early May, although sediment pigment concentrations indicated a continual but low input. Benthic oxygen consumption represented 46% of total spring phytoplankton production or 61% of new production and approximately balanced the calculated flux of detrital carbon (C) to the benthos. The impact of detrital C (assumed to be largely phytodetritus immediately after the spring bloom) on the benthos was short lived, being rapidly remineralised, and in turn little spring production would have been available for secondary production, e.g. *Nephrops norvegica*. In such years, benthic production, particularly that of *N. norvegica*, must be supported by phytoplankton production which takes place after the bloom or by detrital C which is advected into the area following the breakdown of the gyre.

**KEY WORDS:** Spring bloom · Benthic mineralisation · Nutrient exchange · Secondary production

## INTRODUCTION

It has been estimated that 83% of all oceanic benthic remineralisation of organically bound nutrients occurs in shelf sediments (Jørgensen 1983). However, quantifying the linkage between water column production and benthic remineralisation may be complicated by the influence of temperature on microbial activity and transport of particulate material by advection before settling.

In the deeper (~90 m) waters of the western Irish Sea, where tidal flows are weak, the annual cycle of solar

heating results in the formation of a region of thermally stratified water (Simpson & Hunter 1974, Richardson et al. 1985, Gowen et al. 1995). Partial isolation of the bottom water results in temperature increases of only ~1.5°C during spring and summer (Gowen et al. 1995). Vertical gradients in density associated with stratification create a cyclonic gyre of near-surface water (Hill et al. 1994). This gyre appears to retain planktonic animals within the western Irish Sea (White et al. 1988, Dickey-Collas et al. 1996, Hill et al. 1996) and may also limit the import and export of water column production into and from the region. As such the western Irish Sea provides a suitable location at which to study the response of the benthos to changes in primary production in the overlying water column.

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An additional feature of the region is the muddy sediment of the gyre which is the habitat for a commercially important *Nephrops norvegica* fishery. The annual yield from this fishery is ~8000 t, which has a value of ~£10 million (Briggs 1997). It is assumed that this *N. norvegica* secondary production is largely dependent on total seasonal primary production (April to September) in the overlying water, which has been estimated as  $140 \text{ g C m}^{-2}$  (Gowen & Bloomfield 1996).

The influence of settling detritus on benthic microbial processes in the western Irish Sea is largely unknown and the aims of the current study were to (1) quantify the productivity of the spring bloom, (2) assess the subsequent impact of this production on benthic respiration and (3) quantify the fate of nutrients in the benthos.

## MATERIALS AND METHODS

**Sample site.** Nine surveys were conducted at a deep (93 m) station in the western Irish Sea (Fig. 1) between February and July 1998 onboard the RV 'Lough Foyle'. Preliminary measurements of sedimentary oxygen uptake, denitrification and sediment particle size distribution were made during cruises on the RV 'Cirolina' in October 1996 and April and May 1997. During each RV 'Lough Foyle' cruise a vertical profile of temperature and salinity was recorded using a Hydro-Bios CTD mounted on a rosette sampler. The CTD was calibrated for salinity by salinometer measurements on discrete water samples and for temperature by reversing thermometers.

**Water column characteristics.** Recording thermistors (Minilog, Hydrosphere UK Ltd, Aldershot, UK) secured to the instrument arm of a U-shaped mooring recorded temperature from a range of depths throughout the study. Data, recorded at 10 min intervals, were averaged to give mean daily water temperature. Water samples for measurement of phytoplankton chlorophyll and dissolved inorganic nitrate (+ nitrite) were collected from depths selected on the basis of the vertical distribution of temperature and *in situ* fluorescence measured by a Chelsea Instruments Mk III Aquatracka fluorometer mounted on the rosette sampler. Chlorophyll was determined using the method of Tett (1987). Known volumes of water between 0.1 and 0.25 l were filtered through GF/F glass fibre filters. Algal pigments were extracted in neutralised 90% acetone for 24 h at 4°C in the dark. Measurements of extracted chlorophyll fluorescence were made (before and after acidification with 8% hydrochloric acid to distinguish phaeopigments) using a Turner Designs Model 10 filter fluorometer. The average depth of the euphotic zone was taken to be 23 m (Gowen et al.

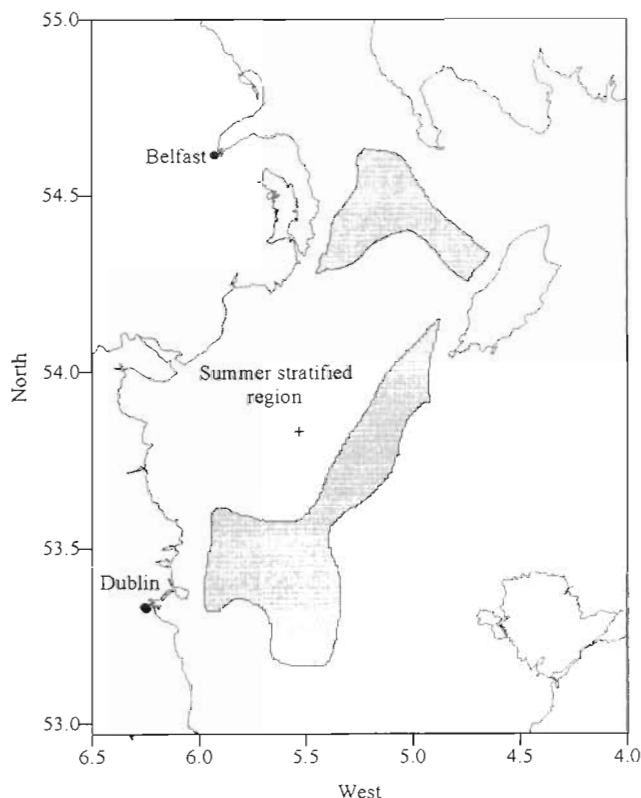


Fig. 1. Map of the western Irish Sea showing location (+) of the sampling site and mooring station. Shaded areas show the approximate locations of the tidal mixing fronts which separate the summer stratified regions from mixed waters

1995) and chlorophyll standing stock within the euphotic zone was determined by interpolation of extracted chlorophyll values. Water samples for determination of dissolved inorganic nitrate (+ nitrite) were stored frozen until analysis using a Bran and Luebbe segmented continuous-flow analyser (TRAACS) employing a colorimetric method (Stewart & Elliot 1996).

**Sediment characteristics. Sediment collection and storage:** Sediment samples were collected using a  $0.1 \text{ m}^2$  box corer (Spartel Ltd). Six large sediment cores (~30 cm deep) were subsampled from the box corer using perspex core tubes (65 cm long  $\times$  8 cm i.d.), each sealed at the bottom with a silicon rubber bung. In addition, small cores of sediment (~12 to 18 cm deep depending on usage) were collected in perspex core tubes (20 cm long  $\times$  2.4 cm i.d.). Four small core tubes (for sulphate reduction) had injection ports at 1 cm intervals, sealed with silicon sealer. Site water collected from close to the sea-bed using the rosette sampler was gently reintroduced over the surface of each core to give a final volume of ~500 ml in the large cores and 100 ml in each of the small cores. The cores were

completely submerged in aerated site water at *in situ* temperature and allowed to re-equilibrate for 2 to 3 h.

**Sediment particle size and porosity:** Particle size distribution was measured in a single small sediment core extruded and sectioned at 1 cm depths from 0 to 10 cm during May 1996. The sections were rinsed with deionised water to remove salt, freeze-dried and weighed. Each sample was then completely re-suspended in deionised water, using an ultrasonic bath to thoroughly disperse the particles and wet sieved through stainless steel mesh from 2 mm to 63  $\mu\text{m}$  (Endecotts Ltd, London, UK). Each fraction was re-dried and expressed as a percentage of the original total dry weight. A single small sediment core was used to determine porosity at 0–5 cm, 6–10 cm and 11–15 cm on each sampling occasion in 1998. Known volumes of sediment were extruded, weighed, dried to a constant weight and then reweighed.

**Sediment organic carbon, total nitrogen and chlorophyll pigments:** Organic carbon, total nitrogen and sediment pigment concentrations were measured in the upper 1 cm of small sediment cores collected on each occasion. In July 1998, a depth profile (0–10, 20 and 30 cm) of pigments was measured. For organic C and N, samples were stored frozen. Before analysis using a Carlo Erba NA 1500 NC, CHN analyser, samples were homogenised with hydrochloric acid (5 ml 1 M) to remove carbonate. Small sediment cores were subsampled using a 50 ml syringe barrel, extruded, and 1 cm depth horizons collected. Pigments were extracted for 24 h in the dark using acetone (40 ml, 90%) and measured by the fluorometric method described above. Sediment pigments were expressed as mg chlorophyll or phaeopigment  $\text{m}^{-2}$  for each 1 cm thick depth horizon.

**Sediment porewater concentrations of sulphate:** Two small sediment cores were used to determine porewater concentrations of sulphate at the same depths as the porosity measurements. The extruded sediment samples were centrifuged ( $1050 \times g$  for 5 min) and the supernatant drawn off with a syringe, filtered and frozen as above. Sulphate concentrations were analysed by ion exchange chromatography (series 2000 i, Dionex Corp, Sunnyvale, California, USA), with a 1.7 mM  $\text{NaHCO}_3$  and 1.8 mM  $\text{Na}_2\text{CO}_3$  eluent, at a flow rate of 3  $\text{ml min}^{-1}$  and a 0.07% solution (v/v) of concentrated  $\text{H}_2\text{SO}_4$  regenerant at a flow rate of 8  $\text{ml min}^{-1}$ . Peak areas of samples were compared to those of known standards.

**Sedimentary rate measurements. Oxygen uptake:** Three of the large core tubes were capped and completely water-filled to exclude air bubbles. A mid-water-column sample (20 ml) was then drawn off into a gas-tight syringe, gently transferred to an Exetainer (12 ml, Labco Ltd, High Wycombe, UK) and fixed for

'Winkler' analysis of dissolved oxygen. The water column in each tube was stirred with an induction motor driving a magnetic follower. The rates of benthic  $\text{O}_2$  uptake were measured using dissolved  $\text{O}_2$  electrodes connected to a computer via a 6 channel oxygen meter (Nedwell & Trimmer 1996). The onscreen computer logging enabled continuous monitoring of the oxygen levels in the water column and further facilitated statistical analyses for linearity with respect to time. Significant rates of oxygen uptake ( $p < 0.05$ ) could usually be determined within 4 h.

**Nutrient exchange:** The remaining 3 large core tubes were capped, but a headspace (50 ml) was left in place. Triplicate water samples (500 ml), with no sediment present, were controls for water column processes in the absence of sediment-water exchange. An air stream was then attached to each cap to aerate and gently mix the water column. A water sample (20 ml) was taken from each flux chamber through a sample port, filtered (0.2  $\mu\text{m}$  Minisart Plus™, Sartorius UK Ltd) and frozen at  $-20^\circ\text{C}$  prior to analyses, and then at every 2 to 4 h for 24 h. On each occasion samples were analysed for nitrate, nitrite, ammonium, urea, silicate and phosphate using the TRAACS analyser as described above.

**Sulphate reduction:** Four of the small sediment cores were used to measure rates of sulphate reduction using a  $^{35}\text{SO}_4^{2-}$  radiotracer technique (Sorokin 1962). Each core was injected at 1 cm intervals down to 15 cm with sodium  $^{35}\text{S}$ -sulphate solution (10  $\mu\text{l}$ ; 37 kBq [ $1 \mu\text{Ci}$ ], specific activity 38.6 TBq  $\text{mmol}^{-1}$ ; Amersham International Ltd, Amersham, UK) made up in ultra high purity (UHP) water. One core was immediately fixed as a  $T_0$  control (see below) and the other 3 cores were incubated for 16 to 24 h at *in situ* temperature. Each core was then extruded, sectioned at 0–5 cm, 6–10 cm and 11–15 cm, homogenised with zinc acetate solution (100 ml of 5% w/v), and frozen at  $-20^\circ\text{C}$ .

After thawing, the fixed subsamples (50 ml) of sediment were digested (Nedwell et al. 1993) to recover both acid volatile sulphides (AVS) and tin-reducible sulphides (TRS); which includes pyrite (Skyring 1985, Nedwell & Takii 1988). The hydrogen sulphide evolved from the digested samples was collected in 2 serial zinc acetate traps (40 ml of 1% w/v). The slurry remaining after digestion of each sediment sample was centrifuged, decanted off, and made up to a known volume (250 ml). Duplicate subsamples from the zinc acetate traps (2 ml) and the residual sediment digests (0.12 ml + 1.88 ml UHP water) were added to scintillation fluid (2 ml Instagel, Packard Instrument Co, UK) and the radioactivity counted in a scintillation counter (Rackbeta, LKB Broma, Sweden) with an external standard to correct for quenching. The ratio of  $^{35}\text{S}$  sulphide to  $^{35}\text{S}$  sulphate was used to calculate rates of sulphate

reduction according to Fossing & Jørgensen (1989), using the measured porosity values and sulphate concentrations.

**Denitrification:** Nine of the small sediment cores were used to measure denitrification rates using the  $^{15}\text{NO}_3^-$  isotope pairing technique of Nielsen (1992). This technique enables differentiation between denitrification supported by the uptake of nitrate from the overlying water ( $D_w$ ) and that coupled to nitrification of porewater  $\text{NH}_4^+$  ( $D_n$ ). Six of the 9 cores were spiked by

addition of  $^{15}\text{NO}_3^-$  (10 mM  $\text{Na}^{15}\text{NO}_3^-$  [99.3 atom %, Europa, Crewe, UK]) into the overlying water, to give a final  $\text{NO}_3^-$  concentration of 40 to 50  $\mu\text{M}$ , and left to equilibrate for 0.5 h (Rysgaard et al. 1995). An initial trial was carried out over a range of  $^{15}\text{NO}_3^-$  concentrations (10 to 50  $\mu\text{M}$ ) to assess the effect of elevated  $\text{NO}_3^-$  concentrations on *in situ* rates of denitrification. Water samples (2 ml) were then collected from all cores to determine the  $^{14}\text{NO}_3^-$ : $^{15}\text{NO}_3^-$  ratio in the overlying water of the treatment cores, filtered and frozen at

$-20^\circ\text{C}$  prior to analyses (see above). The sediment in the 3 reference cores was then gently mixed with the overlying water and a slurry sample (20 ml) carefully drawn off into an Exetainer (12 ml, Labco Ltd, High Wycombe, UK) containing  $\text{ZnCl}_2$  solution (500  $\mu\text{l}$ , 25% w/v) and sealed. The  $^{15}\text{NO}_3^-$  enriched cores were sealed and incubated in the dark at the *in situ* temperature, with gentle stirring ( $\sim 60$  rpm) of the water column for 6 h. The onscreen data logging in the parallel oxygen uptake cores ensured that the concentration of oxygen in the overlying water never fell below 80% of air saturation. Following incubation, the  $^{15}\text{NO}_3^-$  enriched cores were processed in the same way as the reference cores.

All the slurry samples were sent to the National Environmental Research Institute, Silkeborg, Denmark, to be analysed for relative abundance and concentration of  $^{28}\text{N}_2$ ,  $^{29}\text{N}_2$  and  $^{30}\text{N}_2$  on a gas chromatograph coupled to a dual inlet isotope ratio mass spectrometer (Europa Instruments, Crewe, UK). Denitrification rates were calculated according to Nielsen (1992).

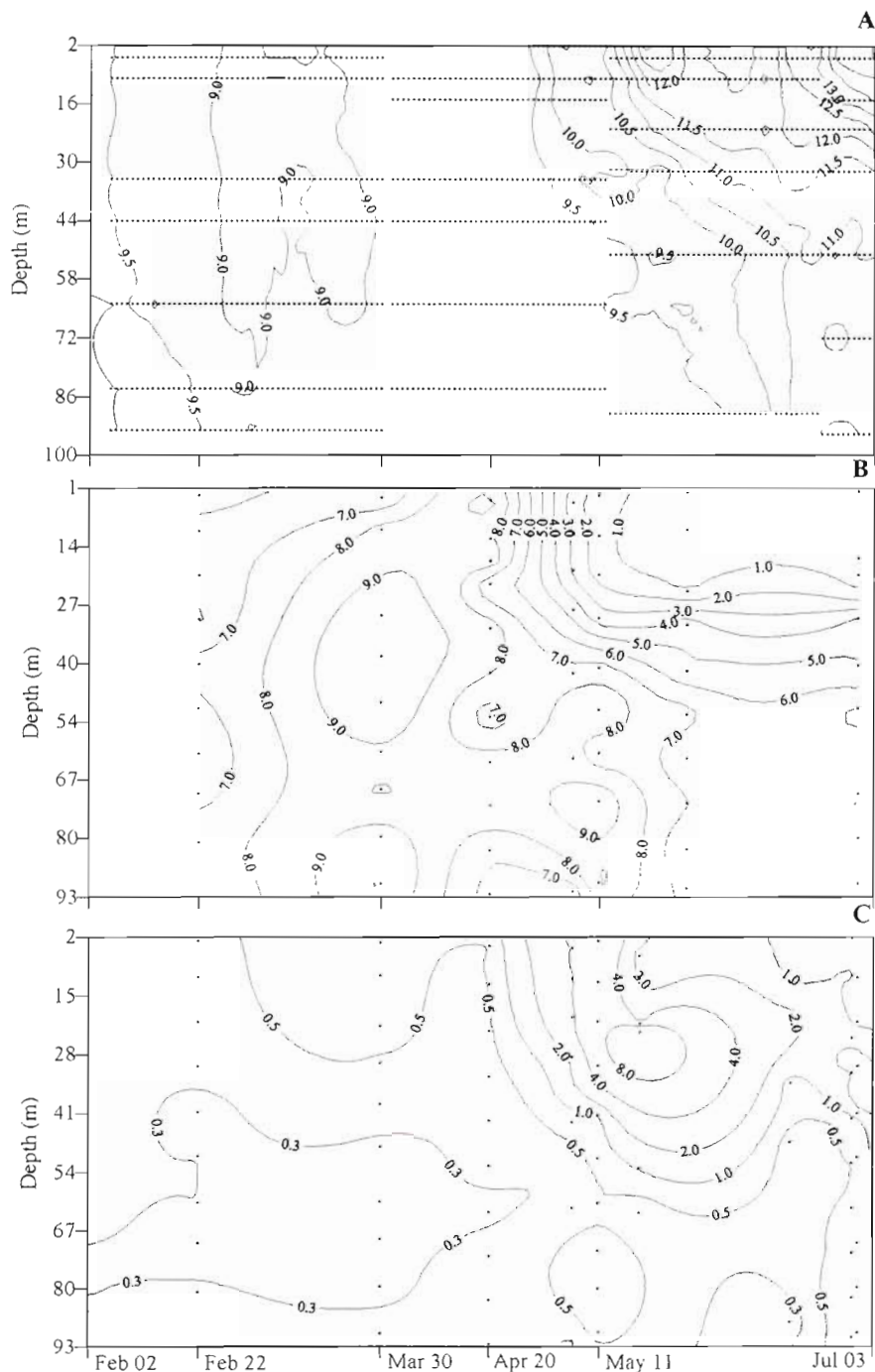


Fig. 2. Contour plots of (A) temperature at 0.5°C intervals, (B) nitrate (+ nitrite) at 1  $\mu\text{M}$  intervals and (C) chlorophyll ( $\text{mg m}^{-3}$ ). The chlorophyll contour intervals are a geometric progression which represents a doubling of biomass

## RESULTS

### Water column characteristics

#### Thermal structure of the water column

There was little evidence of any significant warming of near surface waters during March and early April, and during this period vertical gradients in temperature were  $\leq 0.2^\circ\text{C}$  (Fig. 2A). Thermal stratification of the water column began in late April and by the end of May the surface to bottom difference in temperature was  $2.4^\circ\text{C}$ . Stratification persisted for the remainder of the study, but there was evidence of a mixing event in early June. On June 13 for example, the surface to bottom difference in temperature had fallen to  $1.6^\circ\text{C}$  and the  $10.4^\circ\text{C}$  isotherm extended to the sea-bed. Bottom water temperature increased from  $9.0$  to  $10.7^\circ\text{C}$  between March 1 and July 3.

#### Water column nitrate

Nitrate concentrations reached their winter maxima ( $\sim 9.0 \mu\text{M}$ ) during late March (Fig. 2B). As the spring bloom developed, near surface concentrations of nitrate were depleted and fell to between  $0.46$  and  $0.51 \mu\text{M}$  in June. Bottom water concentrations of nitrate remained relatively constant during the spring bloom period. The reduction in bottom water nitrate concentration coincided with the increase in bottom water temperature at the end of June.

#### Development of the spring bloom

Initiation of the spring bloom coincided with stratification of the water column and the development of a shallow ( $\sim 30$  m) surface mixed layer at the end of April. The bloom lasted approximately 1 mo (Fig. 2C). Peak chlorophyll biomass ( $6.48 \text{ mg chl m}^{-3}$ ) and algal standing stock ( $145.0 \text{ mg chl m}^{-2}$ ) were measured on May 11, following which the bloom declined. Deepening of the chlorophyll isopleths suggested settlement or downward mixing of the bloom in early May (Fig. 2C).

### Sediment characteristics

The sediments were dominated by silt/clay particles (93%) with an average porosity of  $0.77$  (v/v). The average ( $n = 26$ ) organic C content was  $1.5\%$  (dry wt) with a C:N ratio of  $17:1$

(by wt). Total sediment pigment ( $\geq 82\%$  phaeopigment) increased from  $13.36$  to  $57.61 \text{ mg m}^{-2}$  between March 30 and July 3 (Fig. 3). Chlorophyll and phaeopigment decreased with depth in July (Fig. 4). However,  $14.3 \text{ mg m}^{-2}$  of phaeopigment remained at  $30$  cm depth compared to only  $0.72 \text{ mg m}^{-2}$  of chlorophyll (Fig. 4).

### Rate measurements

Maximum rates of sedimentary oxygen uptake ( $1658 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) were measured in early May, but by July oxygen uptake ( $664 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) was similar to that measured in February ( $511 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) (Fig. 5A) and late summer (September 1996). Although there were visible differences between the measured rates of oxygen uptake, only the rates measured during the first cruise in May were significantly different (2-way ANOVA,  $p < 0.05$ ) to those measured on other occasions, i.e. May > April and July. The overall average rate of oxygen uptake, for 1998, was  $924 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1} \pm 119$  (SE,  $n = 18$ ).

The initial denitrification trial showed that there was no significant effect of elevated concentrations of  $^{15}\text{NO}_3^-$  on measured *in situ* rates of denitrification. Denitrification supported by the flux of  $\text{NO}_3^-$  from the overlying water ( $D_w$ ) remained constant from February to late May, but increased significantly during July (2-way ANOVA,  $p < 0.05$ , Fig. 5B). Denitrification coupled to the nitrification of porewater  $\text{NH}_4^+$  ( $D_n$ ) followed a similar trend, with maximal rates being measured in late May and early July. Coupled nitrification-denitrification ( $D_n$ ) made up the greatest fraction of total denitrification, with an average of  $79\%$  ( $D_n$ ) and  $21\%$  for

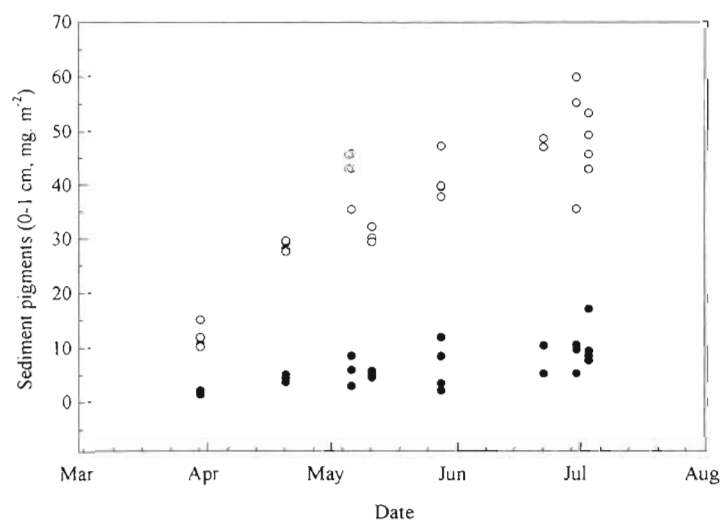


Fig. 3. Surficial sediment pigments (0 to 1 cm), chlorophyll (●) and phaeopigment (○) during spring and early summer 1998



$D_w$ . The rates measured during the cruise in September 1996 are also shown for a late summer comparison.

Rates of sedimentary sulphate reduction (Fig. 5C), measured at all depths, did not vary significantly ( $p < 0.05$ ) from February to late May (11 to 22  $\mu\text{mol SO}_4^{2-} \text{ m}^{-2} \text{ h}^{-1}$  over 0 to 15 cm). However, the rates increased significantly (2-way ANOVA,  $p < 0.05$ ) at 0 to 5 cm and 11 to 15 cm during July (81  $\mu\text{mol SO}_4^{2-} \text{ m}^{-2} \text{ h}^{-1}$ ).

Only the sediment-water exchange rates measured for  $\text{SiO}_3^{2-}$  and  $\text{NO}_3^-$  were significantly greater than zero. The exchange rates for  $\text{NO}_3^-$  were the same on every occasion (ANCOVA) and were therefore expressed as an overall average (10  $\mu\text{mol NO}_3^- \text{ m}^{-2} \text{ h}^{-1} \pm 3$ ; SE,  $n = 93$ ). The exchange rates for  $\text{SiO}_3^{2-}$  were greatest during July (50  $\mu\text{mol SiO}_3^{2-} \text{ m}^{-2} \text{ h}^{-1}$ ) and the rates measured in both early May and July were significantly greater than those measured in March, April or late May ( $p < 0.05$ ).

## DISCUSSION

### Spring bloom

The development of the spring bloom in relation to the onset of stratification is consistent with the vertical processes view of phytoplankton growth. Thus, the timing of bloom initiation is controlled by the underwater light climate as a function of surface mixed layer depth (Sverdrup 1953, Smetacek & Passow 1990, Tett 1990). Chlorophyll standing stock was lower during the 1998 spring bloom compared to other years. For example, in 1997 Gowen et al. (1999) estimated maximum algal standing stock as 199 mg chl  $\text{m}^{-2}$  compared to 145 mg chl  $\text{m}^{-2}$  in 1998. In other respects such as timing and duration (Fig. 2) the 1998 bloom was similar to previous descriptions (Gowen et al. 1995, 1999).

### Sedimentary processes

There are no previous published studies of oxygen uptake, denitrification and sulphate reduction in the sediments of the western Irish Sea. The average rate of oxygen uptake (924  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) in these sediments was consistent with published values from northern European coastal and shelf waters. At 2 muddy sites in the North Sea, Upton et al. (1993) estimated average rates of oxygen uptake as 430 (81 m water depth) and 501 (52 m water depth)  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ . The North Sea sites were not as muddy as the Irish Sea site, with a maximum of only 30% of particles

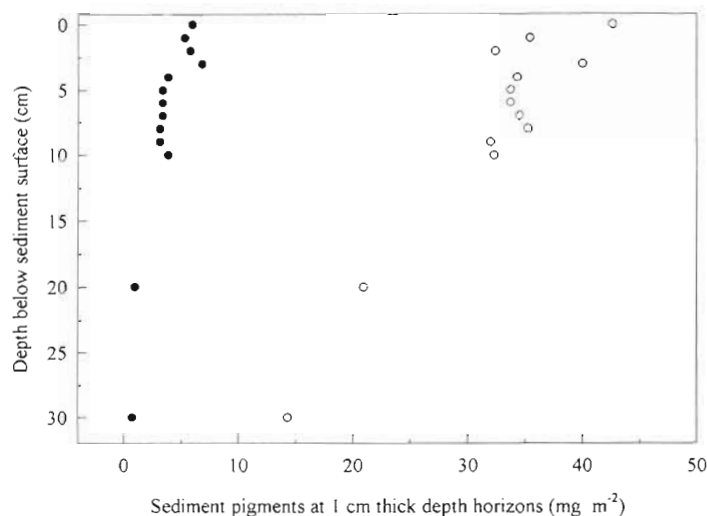


Fig. 4. Sediment pigment depth profile (0 to 30 cm), chlorophyll (●) and phaeopigment (○) measured in July 1998

<63  $\mu\text{m}$ , compared to 93% in the latter. Van Raaphorst et al. (1992) give a seasonal rate of 625 to 1666  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  for the Frisian Front (>20% mud and 39 m depth) in the North Sea. Lohse (1994) reported rates of between 221 and 987  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  for 2 muddy sites (>50% silt) in the Skagen and Helgol Bight (North Sea) respectively.

Of the few studies made on denitrification in temperate marine sediments, only one (Lohse et al. 1996) has used the isotope pairing technique of Nielsen (1992). Lohse et al. (1996) reported an average rate for  $D_w$  of 0.5  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$  for low organic C (0.12% dry wt) sediments in the North Sea, which is at the lower end of the western Irish Sea range of 0.3 to 33  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$ . They also reported an average rate for  $D_n$  of 11  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$ , which is also at the lower end of our range of 3 to 81  $\mu\text{mol N m}^{-2} \text{ h}^{-1}$ . The higher denitrification rates measured in the stratified region reflect the higher organic C content (up to 1.5% dry wt) of these sediments. Lohse et al. (1996) also found that 96% of their total denitrification was coupled to nitrification ( $D_n$ ), which agrees well with our  $D_n$  value of 79%, and supports the hypothesis that in areas of low  $\text{NO}_3^-$  concentrations, e.g. offshore, the percentage of denitrification coupled to nitrification increases (Seitzinger et al. 1980).

Rates of benthic sulphate reduction (0 to 15 cm) were markedly lower (11 to 81  $\mu\text{mol SO}_4^{2-} \text{ m}^{-2} \text{ h}^{-1}$ ) than rates reported in the literature. Upton et al. (1993) give average rates of 160 to 254  $\mu\text{mol SO}_4^{2-} \text{ m}^{-2} \text{ h}^{-1}$  for their 2 muddy sites in the North Sea. Although the data from Upton et al. (1993) were integrated over 0 to 25 cm, compared to 0 to 15 cm in our study, 80% of their activity was measured between 0 and 15 cm. At a high

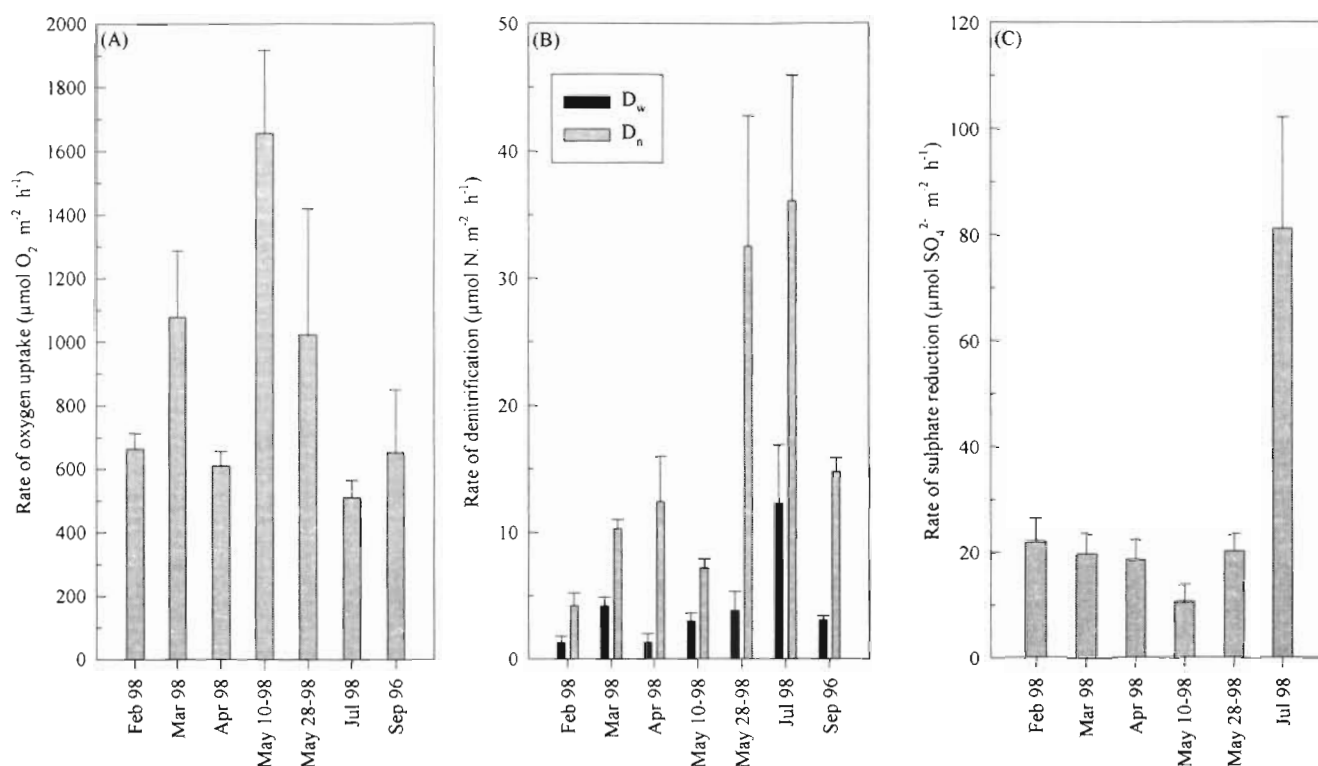


Fig. 5. Sediment respiration rates for (A) oxygen uptake and (B) denitrification, bars indicate standard error,  $n = 3$  and 6 respectively. Additional measurements from September 1996 are also shown for a late summer comparison.  $D_w$ : denitrification supported by the uptake of  $\text{NO}_3^-$  from the overlying water;  $D_n$ : denitrification coupled to the nitrification of porewater  $\text{NH}_4^+$ . (C) Sulphate reduction (integrated over 0 to 15 cm), bars indicate standard error,  $n = 3$

deposition site (70 m depth) in the Kattegat, Jørgensen et al. (1990) measured maximum rates of sulphate reduction at 15 cm ( $\geq 1.6 \text{ nmol SO}_4^{2-} \text{ cm}^{-2} \text{ h}^{-1}$ ) which is an order of magnitude higher than our average rate of  $0.14 \text{ nmol SO}_4^{2-} \text{ cm}^{-2} \text{ h}^{-1} \pm 0.02$  (SE,  $n = 15$ , excluding July) at 15 cm.

In the stratified region measured rates of sulphate reduction were essentially constant from 0 to 15 cm. Typically rates of sulphate reduction peak at  $\sim 5$  cm and then decrease with sediment depth (Jørgensen 1977, Nedwell & Takii 1988, Nedwell 1989, Sagemann et al. 1998). Sulphate is abundant in surficial sediment and the rate of sulphate reduction is more likely to be limited by low availability of organic C or seasonal drop in temperature (Nedwell & Abram 1979, Boudreau & Westrich 1984, Sagemann et al. 1998). As the concentration of sulphate in the Irish Sea sediments was not limiting, and temperature remained essentially constant ( $\Delta T 1.4^\circ\text{C}$ ) the homogeneous distribution of sulphate reduction to 15 cm suggested that labile organic C was distributed relatively evenly throughout the surficial sediment. The depth profile of sediment pigments (Fig. 4) supports this interpretation.

Jørgensen (1982) carried out a detailed survey of both oxygen uptake and sulphate reduction at 58 sta-

tions in Danish fjords and seas. He predicted a 7:1 ratio between the 2 variables for sediments collected from depths of 20 to 200 m, provided oxygen uptake was  $\geq 800 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ . Our average rate of oxygen uptake was  $924 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ , but the ratio of oxygen uptake to sulphate reduction was 42:1 (median). This further suggests that our integrated rates of sulphate reduction are too low and that higher rates of sulphate reduction were occurring below 15 cm. A similar situation was observed by Jørgensen et al. (1990) in the muddy sediment of the Baltic/North Sea transition area. These authors concluded that 50% of sulphate reduction occurred below 15 cm because sedimentation rates were high and there was deep mixing of organic material. In the stratified region of the western Irish Sea, a combination of bioturbation by *Nephtys norvegica* and beam trawling may have been responsible for mixing of the surficial sediment layer and extension of the sulphate reduction zone. This mixing, firstly, oxidises the surficial sediment and reduces the rates of sulphate reduction in these layers; but, secondly, by mixing organic material down into the sediment it also extends downward the depth of the zone of active sulphate reduction. The eventual fate of this buried organic material remains unknown.

### Coupling between the spring bloom and sedimentary processes

The small seasonal change in bottom water temperature (0.1°C up to the end of the spring bloom and 1.4°C overall) provided an opportunity to measure the effect of changes in organic C availability on sediment respiration; effects that can often be masked by seasonal temperature fluctuations. An increase in sediment oxygen uptake was measured in early May, which coincided with deepening of the chlorophyll isopleths (Fig. 2C). This suggests that settling of the spring bloom to the sea-bed fuelled the measured increase in sediment oxygen consumption. Mixing of this organic material throughout the upper 30 cm of the sediment (Fig. 4) in turn stimulated denitrification (late May and early July) and eventually sulphate reduction.

Sediment temperatures in the Antarctic fluctuate around a similarly narrow (although lower) range, e.g. -1.8 to +1°C (Nedwell 1989), to that of the bottom water in the western Irish Sea. Nedwell et al. (1993) concluded that periodic inputs of organic material elevated the organic content of the surface sediment and in turn stimulated oxygen uptake. This organic enrichment of the surface sediment was attributed to the settlement of ice algae following the spring melt. In addition, the proportion of anaerobic mineralisation compared to aerobic mineralisation increased during the winter as organic matter was buried by the amphipod infauna (Nedwell et al. 1993). In the Irish Sea, the proportion of mineralisation via sulphate reduction, compared to aerobic mineralisation, increased from an average of 2% between February and late May to 16% in July. This may have been due to burial of organic material, although the relative importance of bioturbation by benthic fauna and sediment disturbance by trawling has yet to be determined.

There was no significant efflux of  $\text{NH}_4^+$  or urea from the sediment and the sum of  $D_n$  and  $\text{NO}_3^-$  efflux can be assumed to be the same as the total rate of organic N ammonification. Since all the ammonified organic N was in turn oxidised to  $\text{NO}_3^-$ , the total rate of organic N ammonification also represented the rate of nitrification. Denitrification accounted for an average 63% of the ammonified organic N, with the remaining 27% exchanging with the overlying water as  $\text{NO}_3^-$ . Lohse et al. (1996) reported values of 35% and 32%, respectively, for these 2 processes in low organic North Sea sediments. Nitrification and sulphate reduction both accounted for an average of 9% of the oxygen uptake budget (18% in total).

The degree of coupling between water column production during the spring bloom and benthic processes can be assessed by building a simple C budget. Daily total production was estimated from chlorophyll stand-

ing stock using the relationship between stock and water column production (Gowen & Bloomfield 1996, Gowen et al. 1999):

$$\ln \text{ production} = 0.637 \times (\ln \text{ chlorophyll standing stock} + 3.625) \quad (1)$$

and integrating between sampling dates. On this basis total production (new: from winter  $\text{NO}_3^-$ ; and regenerated: from recycled nitrogen; Dugdale & Goering 1967) between February and July was estimated as 44.8 g C  $\text{m}^{-2}$  of which ~70% (31.4 g C  $\text{m}^{-2}$ ) was produced during the spring bloom. As a comparison, spring bloom production can be estimated from the draw down of winter  $\text{NO}_3^-$  and a C:N ratio of 7:1. Between March 30 (the winter  $\text{NO}_3^-$  maximum) and May 11, water column  $\text{NO}_3^-$  decreased by 282 mmol  $\text{m}^{-2}$ , which gives a production of 23.7 g C  $\text{m}^{-2}$ , close to the 31.4 g C  $\text{m}^{-2}$  for total production. The ratio of new to total production (the *f* ratio of Eppley & Peterson 1979) of 0.76 indicates that the spring bloom comprised 76% new production and 24% regenerated production.

By subtracting the mean pre and post spring bloom (February, March, July and September) rate of oxygen uptake (600  $\mu\text{mol m}^{-2} \text{h}^{-1}$ ) from the total integrated oxygen uptake rate the increase in oxygen consumption in response to input of detritus (assumed to be largely phytodetritus immediately after the spring bloom) was estimated as 1.2 mol  $\text{O}_2 \text{m}^{-2}$ . This represents 46% of total spring production (61% of new production) and is comparable to estimates of 17 to 45% in the southern North Sea (Upton et al. 1993) and 55% in the Georgia Bight (Hopkinson & Wetzel 1982).

It is evident that there is sufficient production in the overlying water column to support oxygen consumption in the benthos. However, there are no published measurements of detrital C flux to the benthos for this region of the Irish Sea. An estimate of detrital C flux (Flux  $C_{\text{org}}$ ) to the sea-bed can be obtained using the empirical relationship between production and water depth (Suess & Müller 1980):

$$\text{Flux } C_{\text{org}} = 5.9 \times \text{depth}^{-0.616} \times \text{productivity} \quad (2)$$

Taking water depth to be 93 m, input to the benthos would be 11.3 g C  $\text{m}^{-2}$  (0.94 mol C  $\text{m}^{-2}$ ) or 36% of total spring bloom production, which is similar to the input calculated from oxygen uptake (1.2 mol  $\text{O}_2 \text{m}^{-2}$ ). From an empirical relationship which relates sedimentation to C supply and mixed layer depth (Parsons et al. 1977) the flux of C to the benthos can be estimated as 10.2 g C  $\text{m}^{-2}$  (0.85 mol C  $\text{m}^{-2}$ ) or 32% of spring bloom production. Both empirical relationships underestimate the supply of C to the benthos necessary to support the measured increase in oxygen uptake.

There was little evidence of a large flux of phytodetritus to the benthos during the spring of 1998. Clearly,



there was an input of organic C ( $\sim 1.2 \text{ mol C m}^{-2}$ ) to fuel the increase in sediment oxygen consumption in early May. However, the sediment pigment data (Fig. 4) indicated a continual, but low, input of phytodetritus over the spring. Taken together, our results suggest that in 1998 between 32 and 46% of total spring production reached the benthos, but this input of detritus had only a short-lived impact on the benthos and organic C would have been available to support secondary production, e.g. *Nephrops norvegica*. However, spring bloom production in the stratified region appears to be quite variable. For example, in 1992 and 1993, production was estimated as 51.3 and 38.9 g C  $\text{m}^{-2}$  respectively (data from Gowen & Bloomfield 1996) compared to 28.2 g C  $\text{m}^{-2}$  in 1997 (Gowen et al. 1999) and 31.4 g C  $\text{m}^{-2}$  in this study. It would appear from our results that in some years the spring bloom only plays a minor role in benthic secondary production. In such years, benthic production, particularly that of *N. norvegica*, must be supported by phytoplankton production which takes place after the bloom or by detrital organic C which is advected into the area following the breakdown of the gyre.

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## **Erratum**

### **The spring bloom and its impact on benthic mineralisation rates in western Irish Sea sediments**

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*Mar Ecol Prog Ser 185:37–46*

- On page 45, the word 'little' was omitted in the last paragraph of the text. The third sentence on the page should read 'Taken together, our results suggest that in 1998 between 32 and 46 % of total spring production reached the benthos, but this input of detritus had only a short-lived impact on the benthos and little organic C would have been available to support secondary production e.g. *N. norvegica*.'