



Preface

From physics to fishing over a shelf sea bank

1. Introduction

The research presented in this Special Issue focuses on how seabed topography can drive horizontal patchiness in physical and biogeochemical processes, and organism distributions in a temperate shelf sea during the period of established stratification in summer. The work is based upon data collected during a research cruise aboard the RRS *James Cook* over Jones Bank in the Celtic Sea in summer 2008. Jones Bank was chosen because of its well-defined topography within an otherwise flat region of shelf. The project arose following observations of patchiness in the chlorophyll concentration within the summer sub-surface chlorophyll maximum (SCM) of the Celtic Sea associated with marked increases in internal turbulent mixing over large bank features such as Jones Bank. These sub-surface chlorophyll patches are not apparent at the sea surface and so cannot be detected in satellite imagery. Similar structures in sub-surface chlorophyll have been found to correlate with the distributions of foraging seabirds in the North Sea (Scott et al., 2010). Our aim was to make measurements from the scale of turbulent microstructure, through the biogeochemical rates and phytoplankton distributions, up to the distributions of fish and seabirds. We were motivated to determine what aspects of the shelf system responded to the bank, and what causative links there may be between the physical perturbation caused by the bank and the attraction of the bank for marine top predators, including fishing fleets. In this preface to the Special Issue we will describe the physical and biological environment of the Celtic Sea, using earlier data to highlight the likely effects of a bank on shelf sea structure, and set the context and pose the questions addressed by the papers in this issue. We then summarise the findings of the research, and provide a synthesis describing why banks in a stratified shelf sea may attract mobile marine predators.

2. Physical and biogeochemical environment

The Celtic Sea is a shallow, temperate shelf sea on the north-western European continental margin. Geographically it is bounded to the north by St. Georges Channel and the Irish Sea, to the east by the English Channel, to the southeast by the Bay of Biscay, and to the west and southwest by the edge of the continental shelf and the northeast Atlantic Ocean (Fig. 1). Tidal current amplitudes at spring tides in the Celtic Sea are typically $u = 0.4\text{--}0.6\text{ m s}^{-1}$, with spring tidal flows about twice those at neap tides. When combined with water depths between $h = 100$ and 200 m , this results in the whole Celtic Sea stratifying in response to solar radiation between April and November, with the warm surface

layer of this stratified region bounded by tidal mixing fronts (Simpson and Hunter, 1974) (Fig. 2a). Net heat loss and convective overturning returns the water column to a fully mixed state through autumn and winter. This basic seasonal shift between mixed and stratified states is a fundamental control on the cycle of primary production in the Celtic Sea, similar to other temperate shelf seas (Tett et al., 1993; Thomas et al., 2003). As stratification is established in April an initial surface layer nitrate concentration of about 8 mmol m^{-3} supports a spring phytoplankton bloom. The bloom is typically dominated by diatoms (Fasham et al., 1983; Pingree et al., 1976), with rates of carbon fixation reported at about $15\text{ mg C m}^{-3}\text{ h}^{-1}$ (Pingree et al., 1976), or $1.8\text{ g C m}^{-2}\text{ d}^{-1}$ assuming a 10 m surface layer and 12 h of daylight. Surface layer nitrate is rapidly consumed by the bloom.

In summer, surface waters of the stratified water column have very low phytoplankton biomass (Figs. 2b and 3), with primary production limited by nitrate and phytoplankton growth using regenerated nitrogen. New production occurs in the thermocline in a sub-surface chlorophyll maximum (SCM) (Fig. 3). This SCM is a persistent feature extending 500 km from the shelf edge to the tidal mixing front at the entrance to the Irish Sea (Hickman et al., 2012; Holligan et al., 1984). Daily rates of carbon fixation within the SCM have been observed at $6\text{--}35\text{ mg C m}^{-2}$ (Hickman et al., 2012), with the phytoplankton community consisting of small prokaryotes in the upper SCM and larger eukaryotes deeper in the SCM (Hickman et al., 2009). Negligible nitrate in the surface mixed layer suggests that the phytoplankton in the SCM are able to take up all of the turbulent nitrate flux that is mixed upward from the lower layer into the thermocline, and that a measurement of the turbulent nitrate flux indicates a limit on the potential carbon fixation within the SCM (Sharples et al., 2001). Away from the effects of steep seabed topography typical fluxes of nitrate into the base of the SCM have been measured to be $1\text{--}2\text{ mmol m}^{-2}\text{ d}^{-1}$ (Sharples et al., 2001, 2009). However, an attempt at measuring nitrate fluxes over a steeply sloping bank suggested a localised increase in the flux by an order of magnitude (Tweddle, 2007). Transect surveys of thermocline and chlorophyll structures over banks in the Celtic Sea provided evidence of elevated chlorophyll concentrations within the thermocline (Fig. 4, upper panels), and an increase in chlorophyll within the bottom mixed layer (Fig. 4, lower panels). The implication of these surveys is that seabed banks have marked biogeochemical signatures within the thermocline and bottom mixed layer, but without any clear signal in surface imagery. As the surveys were being carried out it became apparent that the region over the banks was visited by fishing vessels more frequently than areas to the southwest in deeper shelf water. This anecdotal observation was supported with quantitative

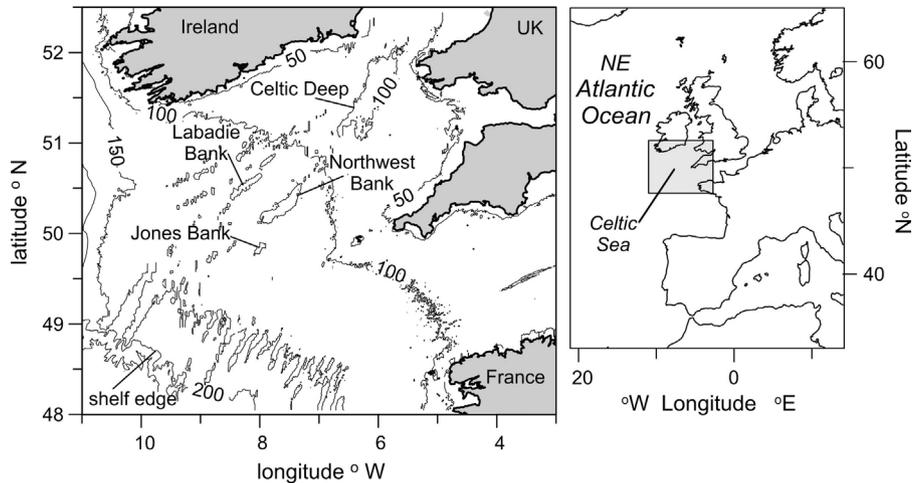


Fig. 1. Location and bathymetry of the Celtic Sea off NW Europe. The shelf edge lies along the 200 m isobath. Locations of key bathymetric features referred to in this issue are marked. Bathymetry is based on the Olex database.

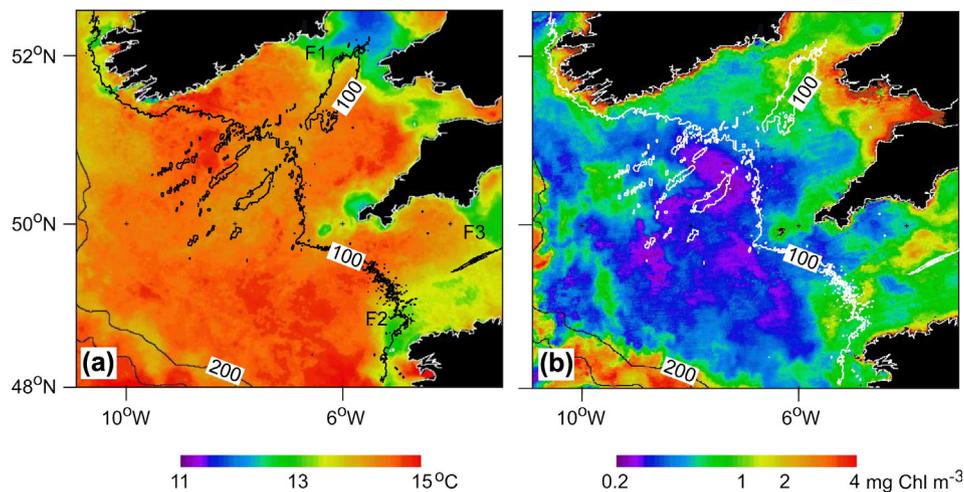


Fig. 2. (a) Sea surface temperature (SST) and (b) surface chlorophyll images of the Celtic Sea. The images are composites over 12th–18th July 2005, and are typical for summer. The sharp horizontal temperature gradients are the tidal mixing fronts: F1 in St. Georges Channel, F2 around Ushant, and F3 in the Western English Channel. In (a) and (b) the 100 m isobath, based on the Olex database, illustrates the field of banks in the central Celtic Sea. Images courtesy of NEODAAS, Plymouth Marine Laboratory, UK.

evidence (e.g. see [Sharples et al., 2013](#)), which raised the question of why the area was particularly attractive to fishing fleets. Was there a connection between the strong turbulent mixing we observed over the banks and the fishing activity? Was this connection made via the biogeochemistry, with phytoplankton responding to the high nitrate fluxes, or caused perhaps by a more direct mechanical link between turbulent mixing and the interactions between predators and prey? These ideas formed the basis for designing the research carried out during cruise aboard the RRS *James Cook* in summer 2008, and this Special Issue summarises the results.

3. Questions addressed in the Special Issue

The aim of the work presented in this issue was to determine what, if any, mechanisms link the physics of internal waves and mixing over the bank to the use of banks as preferred fishing grounds. The observations were based initially around 4 key sites over (MS1, MS2, MS3) and away from (MS4) Jones Bank ([Fig. 5](#)). A fifth site, MS5, was incorporated during the cruise as a site upstream in the mean flow and so uninfluenced by Jones Bank. We

address the following questions, with the relevant contributions noted in brackets.

- (i) How does the bank perturb the physical environment, compared to regions of the Celtic Sea with relatively flat seabed? How is the mixing within the interior of the stratified water column altered, and how far from the bank is the influence of the mixing seen? ([Palmer et al., 2013](#); [Inall et al., 2013](#)).
- (ii) Does the localised mixing generated by the bank lead to significant changes in the biogeochemistry? For instance, by how much is the nitrate supply to the thermocline increased; is there a measurable increase in pelagic primary production in response to the nitrate supply; is there a change in microbial activity in the bank sediments arising from the downward flux of organic matter from the SCM? ([Tweddle et al., 2013](#); [Davidson et al., 2013](#); [Larsen et al., 2013](#)).
- (iii) How patchy is the fishing vessel activity within the Celtic Sea? Are individual banks specifically targeted by fishers? ([Sharples et al., 2013](#)).

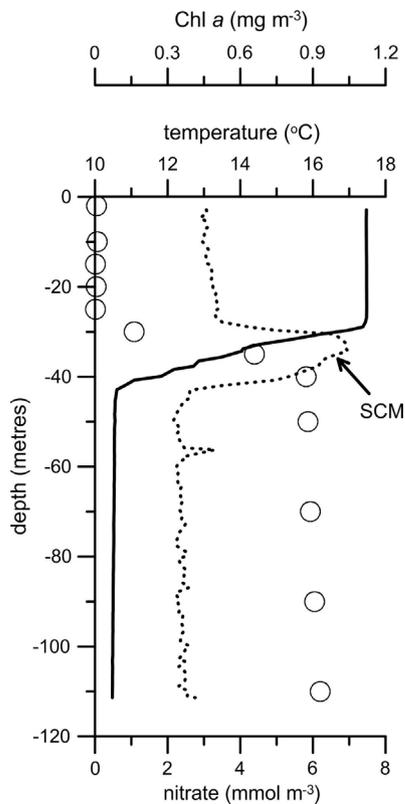


Fig. 3. An example of a vertical profile of temperature (solid line), chlorophyll (dashed line) and nitrate (open circles) in the Celtic Sea. The profile was collected on July 29th 2005 at a position NE of Jones Bank (50°02.36'N, 07°38.28'W).

- (iv) Does the bank have a distinct assemblage of animals (seabirds, fish, epibenthic fauna) compared to regions of flatter seabed? Do any species contrasts have any commercial relevance to the fishing fleets? (Scott et al., 2013; Martinez et al., 2013; Ellis et al., 2013).
- (v) Are there contrasts in animal behaviour over the bank? For instance, do we see changes in the foraging by seabirds over the bank; is fish schooling behaviour different over the bank compared to away from the bank? (Scott et al., 2013; Embling et al., 2013).
- (vi) What mechanisms are likely in driving any contrasts in animal or fishermen distribution or behaviour? For instance, are animals responding to perturbations in the biogeochemistry (e.g. enhanced primary production) driven by the bank's physics? Alternatively, does the physics of the bank more directly affect the distributions and behaviour of prey species and so influence predator foraging success?

Questions (i) to (v) are addressed in the following 10 papers. Here we summarise the findings of the Special Issue, and attempt to provide answers to the final question.

4. Summary of results

4.1. The physical environment

A towed CTD (Scanfish) section through the Celtic Sea (Fig. 6) illustrates the typical summer temperature structure through the region encountered during the 2008 cruise. The entire area was thermally stratified, though with substantial variability in the thickness of the thermocline. A relatively broad thermocline close to the shelf edge was the result of a breaking internal tide and

strong internal mixing (e.g. Inall et al., 2011; Pingree et al., 1984). The thermocline gradually sharpened further on the shelf, with much of the area having a warm surface mixed layer of about 20 m thickness.

Over Jones Bank there was an indication of a slight warming of the bottom layer and a small increase in chlorophyll concentration (Tweddle et al., 2013). These temperature and chlorophyll signals, an indication of mixing of water from the base of the thermocline into the bottom mixed layer, were not as strong as those seen during preliminary investigations in 2005. However, high resolution moored measurements of the thermal structure of the water column during 2008 (Palmer et al., 2013) showed hydraulic control of the flow over the top of the bank and very strong internal wave oscillations over the bank top and slopes. Thermocline displacements of up to 40 m (half the water depth) were seen around spring tides. Such extreme thermocline oscillations were absent during neap tides. They were also very localised over the bank, with internal wave amplitudes decreasing away from the bank crest. The waves were never seen being generated at or reaching a site about 25 km away from the bank in an area of relatively flat seabed. Velocity microstructure measurements over the bank slope (Palmer et al., 2013) indicated these spring tide hydraulic jumps to be associated with pulses in turbulent dissipation throughout the bottom mixed layer and into the thermocline, with tidally-averaged thermocline turbulence dissipation rates $3.3 \times 10^{-4} \text{ m}^2 \text{ s}^{-3}$ – $1.9 \times 10^{-3} \text{ m}^2 \text{ s}^{-3}$. The larger internal waves seen over the bank crest suggest that turbulent dissipation was probably much higher further up the bank. In the absence of these hydraulic jumps, either away from the bank or alternatively over the bank during a neap tide, thermocline turbulent diffusivities averaged over a tidal cycle were about $2.8 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$, similar to values seen elsewhere on the NW European shelf away from steep seabed topography (Rippeth et al., 2005; Sharples et al., 2001).

The dye dispersion experiment conducted during the work in 2008 (Inall et al., 2013) highlights the fate of patches of mixed thermocline water as they were advected away from the bank in the mean flow. The vertical diffusion of dye out of the patch was consistent with the microstructure measurements away from the bank, while horizontal dispersion indicated limited spreading of the dye patch on time scales of up to about 2 days. Much of the horizontal change in the dye patch was driven by shear dispersion, arising largely from the strong winds experienced during the cruise.

The overall picture provided by the physics measurements is of the bank periodically shedding patches of thermocline water that have experienced turbulent mixing by lee waves 1–2 orders of magnitude greater than the background value away from the bank. The strength of the vertical turbulent mixing at the thermocline is dependent on the spring-neap tidal cycle with high vertical mixing associated with spring tides. The storm at the beginning of the cruise, coinciding with a strong spring tide, showed that thermocline turbulent mixing could reach 2 orders of magnitude above the typical value away from the bank. Drift and spreading of these patches of mixing-influenced thermocline water is controlled by mean flows and vertical current shear set up predominantly by the wind.

4.2. Bank influences on biogeochemistry

Preliminary observations in 2005 had suggested that the subsurface chlorophyll maximum (SCM) within the thermocline was enhanced over banks in the Celtic Sea, indicating that the phytoplankton were able to grow in response to the nutrient supply driven by the lee wave mixing (e.g. Fig. 4). It was hypothesised that the vertical turbulent fluxes of nutrients into the SCM over the bank would be significantly increased as a result of the increased

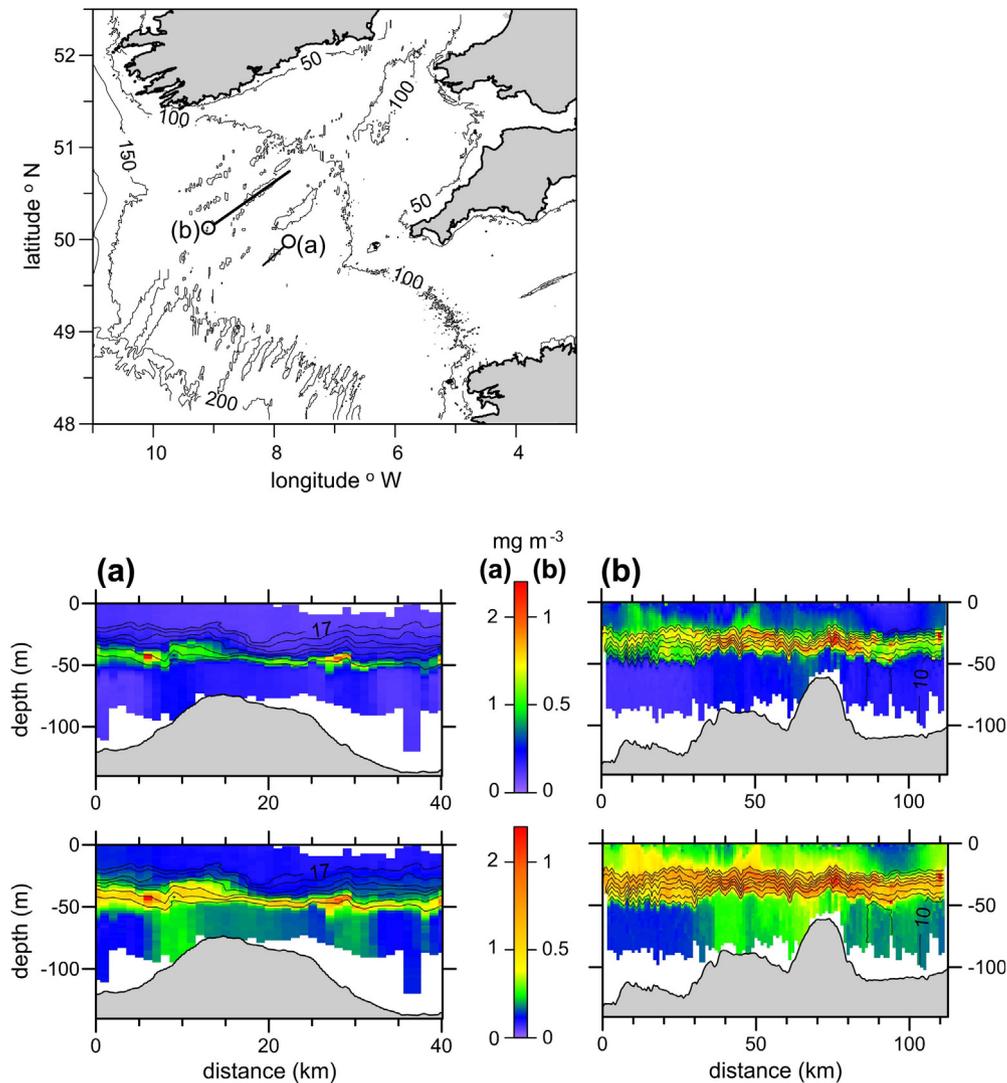


Fig. 4. Along-bank transects of temperature (lines, contoured every 1°C) and chlorophyll concentration (coloured, mg m^{-3}) for (a) Jones Bank and (b) Labadie Bank. Data were collected in July 2005 using the Seasoar towed undulating vehicle, with a horizontal resolution of about 500 m. The transect positions are shown in the map, with the open circle marking the start of the tow, bathymetry based on Olex. For each of (a) and (b) the upper panel uses a linear chlorophyll scale, while the lower panel uses a non-linear scale to highlight the detail at low chlorophyll concentrations.

internal mixing, and the work in 2008 was aimed at quantifying this nitrate flux and detecting whether or not rates of primary production were higher over the bank compared to over adjacent flat regions of the seabed.

Combining the velocity microstructure measurements (Palmer et al., 2013) with measurements of inorganic nutrients clearly showed large increases in turbulent nutrient fluxes to the SCM over the bank (Tweddle et al., 2013). Fluxes into the SCM at neap tides over the bank were about $1 \text{ mmol m}^{-2} \text{ d}^{-1}$, slightly less than that seen away from the bank (about $2 \text{ mmol m}^{-2} \text{ d}^{-1}$). Spring tides over the bank showed substantially increased nitrate supplies to the SCM, between 8 and $50 \text{ mmol m}^{-2} \text{ d}^{-1}$. A response of the phytoplankton productivity over the bank arising from the lee wave mixing and nitrate supply was, however, not clear in the observations of carbon fixation rates (Davidson et al., 2013). However, a model estimate of the impacts of mixing over the bank suggested that any productivity increase over the bank was likely to have been masked by the strong mixing caused by the storm at spring tides (Davidson et al., 2013). The only significant contrast in phytoplankton productivity seen during the cruise was a high growth rate of large phytoplankton (dominated by *phaeocystis*)

during the first spring tide and strong winds. The model also showed that the mean eastward flows advecting water influenced by the bank would show a productivity response to the nitrate supply about 10 km downstream. A peak in the rate of primary production could have occurred between the bank and the flat sampling site, 25 km to the south east, and so been missed by the station sampling. Evidence in support of the downstream impact of bank lee wave mixing is provided by a cross-bank Scanfish survey carried out on the night of July 13th 2008 (Fig. 7). Based on the mean drift indicated by the dye release experiments (Inall et al., 2013) there is a marked increase in SCM chlorophyll concentration downstream in the mean flow from the bank, with a broad patch of high chlorophyll concentration situated about 15 km away from the bank. The strong winds between July 6th and 7th influenced the whole region, and so the localised patch of chlorophyll is not thought to be a result of wind mixing, which would be expected to affect the thermocline everywhere. A widening of the base of the thermocline on the downstream side of the bank suggests that the water had been influenced recently by interior mixing, followed by advection of the mixing-influenced water to the south or southeast.

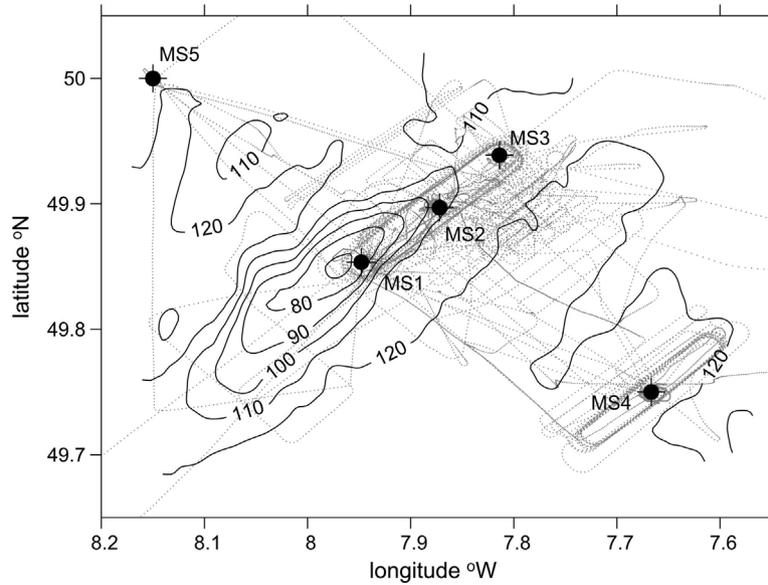


Fig. 5. Main station positions over Jones Bank (see Fig. 1 for general location of Jones Bank in the Celtic Sea). MS1: crest of the bank, MS2: northeast slope of the bank, MS3: bottom of the bank, MS4: flat seabed away from the bank, MS5: flat seabed away from the bank and upstream in the mean flow. Isobaths are contoured based on the underway echosounder measurements of depth, with the ship's track indicated by the grey dots.

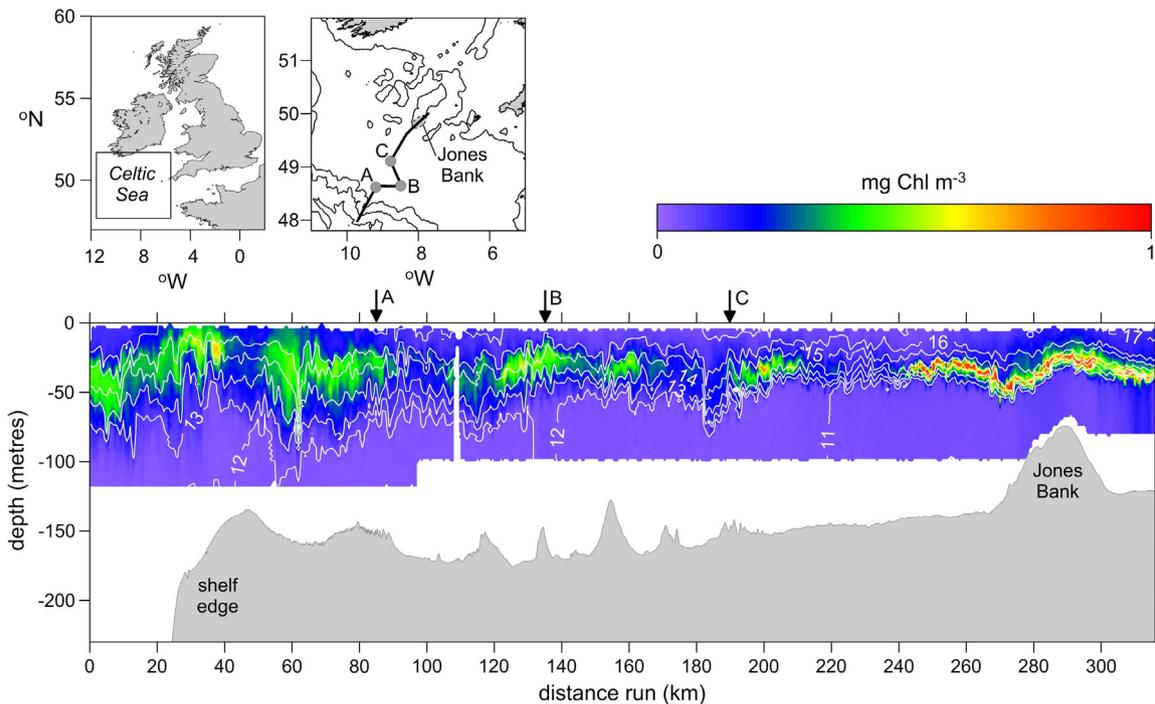


Fig. 6. Section of temperature (line contours) and chlorophyll concentration (colours) observed using a towed Scanfish CTD. The wavelength of the CTD undulations was about 1 km. Note that calibration of the CTD chlorophyll fluorescence, based on samples mainly around Jones Bank, is not expected to be valid close to the shelf edge because of changes likely in phytoplankton community and physiological status.

As well as the possibility of increasing pelagic primary production via the turbulent flux of nitrate over the bank, it was also hypothesised that the corresponding flux of organic material into the bottom waters over the bank may have an effect on the benthic ecosystem. If the bank was also seen to have a distinct benthic or epibenthic ecology compared to the flatter shelf, then the enhanced turbulent mixing over the bank could be implicated in altering the ecology via the supply of organic material to the bottom water. The basic metabolic response of the benthic microbial

community was assessed during the cruise in 2008, comparing the rates of carbon mineralisation and also measuring the flux of recycled nitrogen back into the bottom waters, both over the bank and over the flatter shelf region. No significant contrasts between the bank and nearby flatter regions of the shelf were found (Larsen et al., 2013).

There was, therefore, no direct observational evidence that the bank had higher pelagic primary production or that the bank sediments had higher microbial activity. However, the estimates made

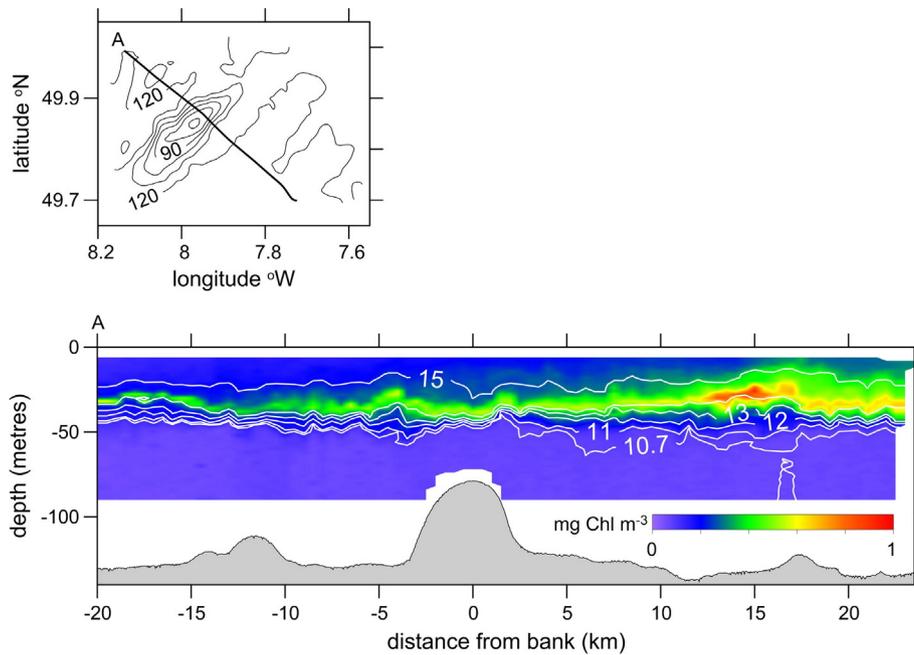


Fig. 7. Cross bank Scanfish section of temperature (line contours) and chlorophyll concentration (colours) on July 13th, 7 days after spring tides. The map indicates the survey track over the bank bathymetry (contoured every 10 m). “A” marks the beginning of the transect survey.

using the numerical model (Davidson et al., 2013) suggest that mixing of nutrients by lee waves over the bank will increase phytoplankton production away from the bank. Whether or not the results of that production are seen over or close to the bank depends on the rate at which the nitrate-enriched thermocline water is advected away from the bank, and the response timescale of the phytoplankton. The biogeochemical importance of banks perhaps instead lies with them providing localised enhanced fluxes of nutrients into the summer SCM which then contribute to phytoplankton growth elsewhere on the shelf as the bank-influenced water is advected away by the mean flow. Mean flows are typically $1\text{--}5\text{ cm s}^{-1}$. Assuming it takes 3–5 days for the phytoplankton to respond to the nitrate supply we might therefore expect new biomass to form within about 20 km of the bank, and then continue to drift downstream. These mean flows are mainly wind-driven, so with prevailing southwesterlies this mixing influence on primary production and phytoplankton biomass is likely to be seen offset to the east and southeast over the field of banks in the central Celtic Sea.

Spring tide nitrate fluxes over the slope of the bank were between approximately $10\text{ and }50\text{ mmol m}^{-2}\text{ d}^{-1}$, a factor of 5–25 times greater than fluxes observed away from the bank. The current meter data from the three moorings over the bank suggested that mixing at the slope site was intermediate between the bank crest and foot (Palmer et al., 2013), so we assume that our measurements on the slope represents a mean for the whole bank at spring tides. If we further assume that the long-term average flux over the bank is half that observed at spring tides, then we can take the bank nitrate flux as being somewhere between 2.5 and 13 times that of the surrounding flatter seabed. If we assume that 10% of the shelf area is composed of banks similar to Jones Bank in height and seabed slope (based on the hydrographic chart of the region (UK Hydrographic Office, 2003)), we can now estimate the integral effect of bank mixing on shelf sea primary production. This suggests that the mixing at shelf sea banks could be supporting an extra 15–120% of new primary production during summer, compared to the same shelf without any bank-driven mixing. Note that

the lower of these two estimates arose from a particularly strong wind event reducing the observed spring tide nitrate flux mainly through a significant reduction in the vertical nitrate gradient.

4.3. Animal and predator distributions and behaviour

Historical data on the distributions of pelagic and demersal fish species, and epifauna, collected with a coarse spatial resolution indicates broad patterns in assemblages. Epifauna show distinct assemblages in the northern Celtic Sea, central Celtic Sea, and two assemblages along the shelf edge (Ellis et al., 2013). Fish species show a similar separation of assemblages, though perhaps showing more overlap particularly between the deep Celtic Sea/shelf edge and the central Celtic Sea (Martinez et al., 2013). These assemblage distributions were based on fish landings and on regular fisheries research surveys. Our work in 2008 used a finer resolution of sampling by comparing assemblages over Jones Bank with those found over an adjacent region of flatter seabed, in order to assess whether or not the localised physics of the bank might influence animal distributions. Some species of fish were found to be very habitat-selective, for instance haddock were observed only over the top of the bank while *Nephrops norvegicus* were most abundant on the flatter areas of seabed (Martinez et al., 2013). The reasons for such habitat selectivity are not always clear. For a species such as haddock, a more detailed assessment of its prey distributions against the contrasts in physical environments may in the future provide some insight into their apparent preference for the top of the bank. Sediment type preferences may provide an explanation for differences in epifauna between the bank and flat seabed (Ellis et al., 2013). *Nephrops* have a preference for muddy sediment substrate, which could result in a tendency for them to be found away from the areas over banks that experience the strong flows and turbulence associated with the lee waves and hydraulic jumps. Alternatively, echinoderms tended to occur mainly over the tops of the bank in areas of coarser sediments. The greatest contrast seen in the epifauna was the high numbers of the anemone *Paraphellia expansa* seen on the tops of banks,

though not enough is known about the animal to make any suggestions for why it has such a clear habitat preference.

The behaviour of foraging animals, both fish and seabirds, did show some contrasts that could be related to the physics of the region. Some of the strongest contrasts in fish schooling behaviour were associated with the spring-neap tidal cycle, with more schools found during neap tides than during spring tides. Fish schools deeper in the water column tended to be larger and less concentrated during neap tides, possibly indicating active foraging (Embling et al., 2013). Regardless of the spring-neap cycle, the tops of the bank tended to have more concentrations of fish above the thermocline than was found away from the bank with sampling suggesting that these fish were zooplanktivores. Distributions of zooplankton over the bank tended to be more vertically homogeneous, compared to tighter layer formation away from the bank. In the upper water column it is possible that the most important contrast between the bank and the flatter seabed areas is the periodic occurrence of the strong internal waves, potentially providing a physical transport and mixing mechanism to disrupt zooplankton predator-avoidance strategies such as diurnal migration and forcing them up towards the surface (Embling et al., 2013; Stevick et al., 2008). There were also significant contrasts between the behaviours of two key seabird species that serve to highlight the potential role of bank-driven internal waves in prey capture (Scott et al., 2013). The European storm petrel, a surface-foraging zooplanktivore, showed a clear preference for the tops of banks, where we have suggested that the large internal waves provide a mechanisms for transporting zooplankton towards the sea surface. By contrast the gannet, a more generalist feeder and capable of reaching considerable depth during dives, did not show any preference to the banks but instead had foraging behaviour related more to the spring-neap tidal cycle and the distribution of fish schools. While overall the gannets did not show a preference for foraging over banks, when they were seen over banks their foraging appeared to occur at the times of strong internal wave activity at spring tides, suggesting a response to the increased prey availability or visibility provided by the vertical movement of water.

4.4. Fishing activity in the central Celtic Sea

The location and timing of fishing activity is driven by experience and the historical knowledge of skippers (Pålsson, 2000). Analysis of fishing vessel position data, using data from the Vessel Monitoring System, has shown that individual skippers have particular geographical preferences for fishing (Sharples et al., 2013). These geographical preferences within the broad central Celtic Sea fishing region could be driven by fish species or behaviour contrasts observed between the banks and adjacent flat areas (Embling et al., 2013). There was no overall preference for fishing over banks compared to adjacent flatter areas of seabed; fishing activity was evenly distributed throughout the region, over and between a number of seabed banks (Sharples et al., 2013). There was evidence that some skippers fish more at neap tides than close to spring tides, probably driven by which species are being targeted (e.g. fishing for *Nephrops* is significantly diminished at spring tides) or gear type (gill netters often avoid stronger currents to avoid set-down of the nets). There is no suggestion, therefore, that the physics of lee waves over banks aids fishing directly through prey re-distribution. The spatially uniform distribution of fishing over the field of banks instead suggests that the advantage to the fishing skippers is through a similarly broad effect of the banks. In Sharples et al. (2013), it was suggested that an overall increase in biological productivity underpins the fisheries, with large, bank-driven fluxes of nutrients into the thermocline supporting increased primary production coupled with physical dispersion away from the mixing sites. The necessary increase in zooplankton

concentrations, responding to this primary production and providing a trophic link to fish, was justified based on the typical residence time of the water within the bank region (Sharples et al., 2013). Increased zooplankton concentrations were supported qualitatively by contrasts in zooplankton acoustic signals over the banks compared to the flatter, deeper shelf to the southwest (Embling et al., 2013). This suggestion of fish and fishing being supported by increased primary production contrasts with the underlying supporting mechanisms in the two other main Celtic Sea fishing regions: the shelf edge, where internal tides driving a shift in the phytoplankton community structure and cell size, and the Celtic Deep where it is likely that tidal flow characteristics are the key determinant by setting a seabed habitat suitable for *Nephrops* (Sharples et al., 2013).

5. Conclusions

Observations during a research cruise in the central Celtic Sea in summer 2008 have shown that seabed banks have a significant effect on the supply of bottom water nutrients into the seasonal thermocline via the generation of lee waves and strong internal mixing. These nutrient fluxes, up to 50 times greater than those typically observed away from banks, are thought to drive increased new primary production within the sub-surface chlorophyll maximum, with mean flows then dispersing the biomass over a wider region. The bank-influenced region is marked by generally higher concentrations of phytoplankton within the thermocline compared to areas well away from the banks, and also higher concentrations within the bottom water caused by turbulent mixing of biomass out of the base of the thermocline.

On the scale of an individual bank and nearby flatter seabed, contrasts were found in the species of fish, the vertical distributions of fish, and schooling behaviour. There was also significant correlation between fish behaviour and the spring-neap tidal cycle. The two main species of seabirds seen in the area also showed bank-off-bank contrasts in foraging. In particular the European Storm Petrel was seen to forage at the sea surface over banks during times of strong lee wave activity, illustrating a direct link between a physical perturbation of the water column and prey availability.

Fishing vessels were found to be very site-specific in fishing activity, probably reflecting the experience of individual skippers combined with species choices. However, there was no overall preference for fishing over individual banks rather than nearby flatter areas of seabed. Instead we suggest that the central Celtic Sea fisheries arise as a response to an overall increase in biological productivity triggered by bank-driven lee waves and an increased supply of nutrients to the primary producers. This contrasts with the likely mechanisms supporting fisheries in other deep water areas of the Celtic Sea, underlining the need for careful determination of the scientific basis for different fisheries, in order to provide robust evidence for the design of Marine Protected Areas and to underpin predictions of how different fisheries might respond to a changing climate.

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References

- Davidson, K., Gilpin, L.C., Pete, R., Brennan, D., McNeill, S., Moschonas, G., Sharples, J., 2013. Phytoplankton and bacterial distribution and productivity on and around Jones Bank in the Celtic Sea. 117, 48–63.
- Ellis, J.R., Martinez, I., Burt, G.J., Scott, B.E. 2013. Epibenthic assemblages in the Celtic Sea and associated with the Jones Bank. 117, 76–88.
- Embling, C.B., Sharples, J., Armstrong, E., Palmer, M.R., Scott, B.E., 2013. Fish responses to tidal variability and internal waves over a shelf sea bank. 117, 106–117.
- Fasham, M.J.R., Holligan, P.M., Pugh, P.R., 1983. The spatial and temporal development of the spring phytoplankton bloom in the Celtic Sea, April 1979. *Progress in Oceanography* 12, 87–145.
- Hickman, A.E., Holligan, P.M., Moore, C.M., Sharples, J., Krivtsov, V., Palmer, M.R., 2009. Distribution and chromatic adaptation of phytoplankton within a shelf sea thermocline. *Limnology and Oceanography* 54, 525–536.
- Hickman, A.E., Moore, C.M., Sharples, J., Lucas, M.I., Tilstone, G.H., Krivtsov, V., Holligan, P.M., 2012. Primary production and nitrate uptake within the seasonal thermocline of a stratified shelf sea. *Marine Ecology Progress Series* 463, 39–67.
- Holligan, P.M., Harris, R.P., Newell, R.C., Harbour, D.S., Head, R.N., Linley, E.A.S., Lucas, M.I., Tranter, P.R.G., Weekley, C.M., 1984. Vertical-distribution and partitioning of organic-carbon in mixed, frontal and stratified waters of the English Channel. *Marine Ecology Progress Series* 14, 111–127.
- Inall, M., Aleynik, D., Boyd, T., Palmer, M., Sharples, J., 2011. Internal tide coherence and decay over a wide shelf sea. *Geophysical Research Letters* 38, L23607. <http://dx.doi.org/10.1029/2011GL049943>.
- Inall, M.E., Aleynik, D., Neil, C., 2013. Horizontal advection and dispersion in a stratified shelf sea: the role of inertial oscillations. 117, 25–36.
- Larsen, M., Thamdrup, B., Shimmield, T., Glud, R.N., 2013. Benthic mineralization and solute exchange on a Celtic Sea sand-bank (Jones Bank). 117, 64–75.
- Martinez, I., Ellis, J.R., Scott, B., Tidd, A., 2013. The fish and fisheries of Jones Bank and the wider Celtic Sea. 117, 89–105.
- Palmer, M.R., Inall, M.E., Sharples, J., 2013. The physical oceanography of Jones Bank: a mixing hotspot in the Celtic Sea. 117, 9–24.
- Pålsson, G., 2000. Finding one's sea legs: learning, the process of enskilment, and integrating fishers and their knowledge into fisheries science and management. In: Neis, B., Felt, L. (Eds.), *Finding our Sea Legs: Linking Fishery People and Their Knowledge with Science and Management*. ISER Books, St. John's, Newfoundland.
- Pingree, R.D., Holligan, P.M., Mardell, G.T., Head, R.N., 1976. Influence of physical stability on spring, summer and autumn phytoplankton blooms in Celtic Sea. *Journal of the Marine Biological Association of the United Kingdom* 56, 845–873.
- Pingree, R.D., Griffiths, D.K., Mardell, G.T., 1984. The structure of the internal tide at the Celtic Sea shelf break. *Journal of the Marine Biological Association of the United Kingdom* 64, 99–113.
- Rippeth, T.P., Palmer, M.R., Simpson, J.H., Fisher, N.R., Sharples, J., 2005. Thermocline mixing in summer stratified continental shelf seas. *Geophysical Research Letters* 32, L05602. <http://dx.doi.org/10.1029/2004GL022104>.
- Scott, B.E., Sharples, J., Ross, O.N., Wang, J., Pierce, G.J., Camphuysen, C.J., 2010. Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Marine Ecology Progress Series* 408, 207–226.
- Scott, B.E., Webb, A., Palmer, M.R., Embling, C.B., Sharples, J., 2013. Fine scale biophysical characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanus*) & Storm Petrel (*Hydrobates pelagicus*). 117, 118–129.
- Sharples, J., Moore, C.M., Rippeth, T.P., Holligan, P.M., Hydes, D.J., Fisher, N.R., Simpson, J.H., 2001. Phytoplankton distribution and survival in the thermocline. *Limnology and Oceanography* 46, 486–496.
- Sharples, J., Moore, C.M., Hickman, A.E., Holligan, P.M., Tweddle, J.F., Palmer, M.R., Simpson, J.H., 2009. Internal tidal mixing as a control on continental margin ecosystems. *Geophysical Research Letters* 36, L23603. <http://dx.doi.org/10.1029/2009GL040683>.
- Sharples, J., Ellis, J.R., Nolan, G., Scott, B.E., 2013. Fishing and the oceanography of a stratified shelf sea. 117, 130–139.
- Simpson, J.H., Hunter, J.R., 1974. *Fronts in Irish Sea*. *Nature* 250, 404–406.
- Stevick, P.T., Incze, L.S., Kraus, S.D., Rosen, S., Wolff, N., Baukus, A., 2008. Trophic relationships and oceanography on and around a small offshore bank. *Marine Ecology Progress Series* 363, 15–28.
- Tett, P.B., Joint, I.R., Purdie, D.A., Baars, M., Oosterhuis, S., Daneri, G., Hannah, F., Mills, D.K., Plummer, D., Pomroy, A.J., Walne, A.W., Witte, H.J., 1993. Biological consequences of tidal stirring gradients in the North Sea. *Philosophical Transactions of the Royal Society of London, Series A* 343, 493–508.
- Thomas, A.C., Townsend, D.W., Weatherbee, R., 2003. Satellite-measured phytoplankton variability in the Gulf of Maine. *Continental Shelf Research* 23, 971–989.
- Tweddle, J.F., 2007. *Nutrient Fluxes into the Seasonal Thermocline of the Celtic Sea*. PhD. University of Southampton.
- Tweddle, J.F., Sharples, J., Palmer, M.R., Davidson, K., McNeill, S., 2013. Enhanced nutrient fluxes at the shelf sea seasonal thermocline caused by stratified flow over a bank. 117, 37–47.
- UK Hydrographic Office, 2003. *Western Approaches to the English Channel*. Chart No. 2649.

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