Shelf Sea Biogeochemistry: Nutrient and carbon cycling in a temperate shelf sea water column.

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Abstract.

This special issue presents some of the key findings from the pelagic component of the UK Shelf Sea Biogeochemistry Research Programme, carried out on the northwest European shelf between March 2014 and August 2015. The project aimed to address two issues: (1) how does a temperate shelf sea sustain an annual net drawdown and export of atmospheric CO$_2$ without running out of inorganic nutrients, and (2) what uncertainties in processes or parameterisations within current ecosystem models can be reduced by a coordinated, multi-disciplinary observational programme covering the full seasonal cycle? Working with partners across Europe, the net annual drawdown of atmospheric CO$_2$ over the entire northwest European shelf was confirmed. This demonstrated the context and impetus for a 17-month process study in the Celtic Sea, using a long-term mooring array and several research cruises, addressing shelf sea physics, inorganic and organic nutrient and carbon cycling, and bacterial, phytoplankton and zooplankton roles and dynamics. It was clear from the physics that all the carbon absorbed through the sea surface over one year was not exported to the open ocean. Physical transports were too weak and too slow to transport all the carbon-laden water over a wide shelf sea to the shelf edge within one year. The shelf sea must therefore be able to store carbon in a form that prevents release back to the atmosphere for a timescale that is sufficient to allow more episodic (timescales > 1 year) exchange events to both remove the excess carbon and top-up the shelf pool of inorganic nutrients. The results presented in this special issue illustrate the likely key role of recalcitrant dissolved organic carbon in storing carbon on the shelf and highlight the need for longer-term measurements or monitoring to understand the nature and timing of potentially large but infrequent exchange events between the shelf and open ocean.

1. Introduction.

Shelf seas play a significant role in the global cycling of carbon by the oceans, driving between 10 and 30% of marine primary production, 30 to 50% of inorganic carbon burial and ~80% of organic carbon burial (Bauer, Cai, Raymond, Bianchi, Hopkinson et al., 2013; Liu,
Overall, the present-day shelf seas are a net sink for atmospheric CO$_2$, though this may be a relatively new phenomenon: pre-industrial shelf seas are likely to have been a net source of CO$_2$ to the atmosphere, with the switch to a net sink occurring as a response to anthropogenic increases in atmospheric CO$_2$ (Bauer et al., 2013; Laruelle, Cai, Hu, Gruber, Mackenzie et al., 2018; Mackenzie, Lerman & Andersson, 2004). Thus, shelf seas play a disproportionately important role in global carbon cycling and Earth’s climate relative to their limited geographical area, with their current role a response to anthropogenic forcing.

Shelf seas also provide a range of services to the increasing human populations which live and work in coastal areas. They make a vital contribution to the food supplies required by the global human population, with more than 90% of global fish catches taken from shelf seas (Pauly, Christensen, Guenette, Pitcher, Sumaila et al., 2002). These shallow, coastal seas receive material delivered by river run-off, often including high loads of sediments, nutrients and carbon (Beusen, Dekkers, Bouwman, Ludwig & Harrison, 2005; Seitzinger, Mayorga, Bouwman, Kroeze, Beusen et al., 2010). The shelf seas act as a buffer between rivers and the open ocean, processing river-borne material and reducing the amount that reaches beyond the shelf edge (Izett & Fennel, 2018; Painter, Lapworth, Woodward, Kroeger, Evans et al., 2018; Sharples, Middelburg, Fennel & Jickells, 2017). The type and amount of material that is carried by rivers is sensitive to the human management of catchment areas (Bouwman, Beusen & Billen, 2009) and the extent of wastewater treatment (Van Drecht, Bouwman, Harrison & Knoop, 2009). High nutrient loading arising from agricultural run-off and wastewater release often results in enhanced biological oxygen demand and reduced dissolved oxygen concentrations, to the detriment of coastal ecosystems and fisheries (Diaz & Rosenberg, 2008; Fennel & Testa, 2019; Rabalais, Diaz, Levin, Turner, Gilbert et al., 2010).
It is this combined background of the shelf seas’ central role in the global carbon cycle and climate, the importance of shelf seas to food supply and waste dispersal, and the changes to these roles in response to future human activities that led to the development of the UK Shelf Sea Biogeochemistry research programme, funded through the UK Natural Environment Research Council (NERC) and the UK government Department of Environment Food and Rural Affairs (Defra). As well as water column physics, biology and biogeochemistry, the programme included observational components on sediment biogeochemistry (e.g. (Hicks, Ubbara, Silburn, Smith, Kroger et al., 2017; Kitidis, Tait, Nunes, Brown, Woodward et al., 2017; Thompson, Silburn, Williams, Hull, Sivyer et al., 2017)), iron cycling (e.g. (Birchill, Milne, Woodward, Harris, Annett et al., 2017)) and ecosystem modelling (e.g. (Butenschoen, Clark, Aldridge, Allen, Artioli et al., 2016)).

The papers presented in this Special Issue arise from detailed observational studies of pelagic physics and biogeochemistry across the Celtic Sea on the northwest European continental shelf (Fig. 1), an archetypal temperate shelf environment that undergoes seasonal stratification with distinct spring and autumn plankton blooms (Sharples & Holligan, 2006). The project began with two overarching questions:

1. **How can a shelf sea export carbon to the open ocean without running out of nutrients?** This question arises from a thought experiment of what happens to the nutrients on a shelf if biogeochemical cycling operates with a fixed stoichiometry of carbon to nitrogen to phosphorus (here we assume the Redfield ratio C:N:P of 106:16:1 (Redfield, 1934)). Carbon exported to the open ocean (with its concomitant N and P) is replaced via a CO₂ influx from the atmosphere. There then needs to be one or more processes that fulfill the same role for nutrients, replacing the exported nutrients and allowing the shelf system to continue operating with a fixed stoichiometry. The focus for this excess nutrient supply was on one or more of: non-Redfield carbon uptake (e.g. (Bozec, Thomas, Schiettecatte, Borges, Elkalay et al., 2006)); preferential recycling and shelf retention of nutrients (e.g. (Lonborg,
Davidson, Alvarez-Salgado & Miller, 2009; Toggweiler, 1993)) compared to carbon on the shelf; and excess nutrient delivery from rivers (e.g. (Jickells, 1998)) (if we assume that delivery from the ocean occurs with the same stoichiometry as the biogeochemical cycling on the shelf).

(2) **What key uncertainties in ecosystem model parameterisations, driving data, or calibration/validation data can be ameliorated by a new, coordinated multidisciplinary programme of observations?** A separate project within the Shelf Sea Biogeochemistry programme began shortly after the observational programme was started, with the aim of taking advantage of the planned long time series and process experiments and with a focus on the European Regional Seas Ecosystem Model (ERSEM), e.g. (Butenschoen et al., 2016).

This Preface to the Special Issue summaries some of the key results arising from the water column observational programme, and highlights what the answer(s) to question (1) above may be, indicates some of the results that are relevant to addressing model uncertainties, and finally identifies some key gaps in our understanding of the shelf cycling of carbon and nutrients that remain.

2. **The Observational Programme.**

The broader geographical focus of the Shelf Sea Biogeochemistry programme was on the wide continental shelf areas of northwest Europe, with a process-study focus on the Celtic Sea (Fig. 1). Seasonally stratifying parts of the shelf (the Celtic Sea and western English Channel, the northern North Sea and the Malin Sea, Fig. 1) are net annual sinks for atmospheric CO$_2$. About $6 \times 10^{12}$ mol C are exported to the adjacent northeast Atlantic Ocean, about half of which may be transported below the seasonal pycnocline off the shelf (Borges, Schiettecatte, Abril, Delille & Gazeau, 2006; Wakelin, Holt, Blackford, Allen, Butenschoen et al., 2012). At the scale of the entire northwest European shelf the aim of the project was, via extensive collaborations with other European partners, to assess the net
annual air-sea flux of CO$_2$ alongside the surface ocean biogeochemistry. The Celtic Sea contributes to this overall shelf carbon export (Marrec, Cariou, Mace, Morin, Salt et al., 2015) and was chosen for the focus of the process studies as it enables the full (seasonal) range of shelf processes and environments to be easily reachable over a typical 30 day research cruise.

Figure 1.

Typical summer sea surface temperature image for the northwest European shelf, indicating key observation locations. Dotted lines show approximate coverage of partner transects (either research vessel surveys or repeat lines of ships of opportunity; see (Hartman, Humphreys, Kivimäe, Woodward, Kitidis et al., this issue; Humphreys, Achterberg, Hopkins, Chowdhury, Griffiths et al., this issue)). The process studies took place in the Celtic Sea: WEC is the western English Channel with E1 the WEC observatory long-term mooring (see (Djeghri, Atkinson, Fileman, Harmer, Widdicombe et al., this issue)), CS2 is the shelf edge station, CCS is the location of the mooring array (see (Wihsgott, Sharples, Hopkins, Woodward, Hull et al., this issue)), CD is the northern-most station also used by the benthic Shelf Sea Biogeochemistry project (see (Hicks et al., 2017; Kitidis et al., 2017; Thompson et al., 2017). Image courtesy of NEODAAS, Plymouth Marine Laboratory.
The field programme began in March 2014, with the deployment of an array of moorings at the Central Celtic Sea (CCS) site (Fig. 1). CCS was situated in the middle of the seasonally-stratifying region, about 100 km from the shelf edge and clear of significant fishing activity (e.g. (Sharples, Ellis, Nolan & Scott, 2013)). The moorings provided a total of 17 months of almost continuous data on water column physical structure (temperature, salinity and currents), surface chlorophyll (fluorescence) and nutrients (a Smartbuoy operated by the Centre for Environment Fisheries and Aquaculture Science) and meteorology (operated by the UK Meteorological Office). Station CS2 was an established study site at the shelf edge, where mixing by a breaking internal tide is a key underpinning physical process (e.g. (Sharples, Tweddle, Green, Palmer, Kim et al., 2007)). Station CD (Celtic Deep) was a joint station operated by the pelagic and benthic components of the Shelf Sea Biogeochemistry research programme, and the long-term mooring at E1 provided additional time series in a shallower seasonally-stratifying location. Stations CCS, CS2 and CD were visited several times during each of the pelagic process study cruises; a basic suite of information was collected at CCS and CS2 during cruises operated by the benthic project; station CD was the main process study site for the benthic project and marked the northernmost sampling site for the pelagic process study cruises. A total of 9 research cruises were carried out between March 2014 and August 2015, with the main pelagic process study cruises occurring in November 2014, April 2015 and July 2015.

3. Summary of Key Results.

(Ruiz-Castillo, Sharples, Hopkins & Woodward, this issue) illustrate the underpinning changes in the cross-shelf physical structure, using the CTD transect data from all available cruises. As expected, the shelf stratified in April (2014 and 2015), with stratification then maintained until late December. The salinity distributions from the CTD transects are used to assess the likely rates of horizontal transport across the shelf. Movement of higher salinity water from the shelf edge in towards the shelf interior in summer suggested a mechanism for
the supply of oceanic nutrients, largely a result of wind-driven flows but with a significant contribution from Stoke's drift associated with internal tidal waves. There was a clear indication of cross-shelf transport towards the shelf edge in winter, with the outer 100 km of shelf water potentially reaching the shelf edge to be exchanged with the open ocean. The mean transport of about 1 m² s⁻¹ was a combination of wind-driven transport and an estuarine-like flow driven by the horizontal density gradient caused by differential cooling as the shelf shallowed. (Ruiz-Castillo et al., this issue) also attempted a basic seasonal budget of nitrate at the CCS mooring site, taking into account cross-shelf transports, an estimate of riverine contribution, vertical mixing across the seasonal pycnocline, and uptake during the spring and autumn blooms and within the summer sub-surface chlorophyll layer. Comparing the nitrate available in March 2014 with that found in March 2015, the implication was that 50-62% of the available nitrate in March 2015 was locally recycled (consistent with tight coupling observed within the plankton community (Giering, Wells, Mayers, Schuster, Cornwell et al., this issue)), with the remaining 38-50% either (in descending order) unused during the previous 12 months, supplied via transport from the shelf edge, or contributed by rivers. The latter was estimated to be about 10% of the available nitrate at CCS.

High-resolution oxygen measurements during the spring bloom showed large changes in rates of net community production occurring within just a few hours. The fraction of primary production on the shelf estimated to be available for export (based on net and gross community oxygen production) was found to be 0.25, compared to 0.07 off the edge of the shelf, indicating the importance of primary production on the wide, shallow shelf for carbon export (Seguro, Marca, Painting, Shutler, Suggett et al., this issue). It was found, however, that the phytoplankton community in the spring bloom was made up of nanoplankton (2-20 μm), which differed from expectations of larger spring bloom phytoplankton (i.e. large diatoms) based on earlier work (e.g. (Rees, Joint & Donald, 1999)) potentially lowering the export fraction in April 2015. Calcite production by coccolithophores during the spring bloom was measured to determine the contribution to total bloom carbon fixation that might counter
biological drawdown of inorganic carbon. Only 0.2 to 2% of spring bloom primary production was found to be carried out by the coccolithophores, with strong top-down control on coccolithophore growth as microzooplankton (20-200 μm) removed about 60% of daily calcite production (Mayers, Poulton, Daniels, Wells, Woodward et al., this issue), though the fate of this grazed material (internal dissolution or packaging into fecal pellets) was unknown. An exception to this was a single site in the northern Celtic Sea, where a marked bloom (>2000 cells mL⁻¹) of Emiliania huxleyi accounted for 30% of the total primary production and led to some of the highest reported calcite production rates in the ocean (Daniels, Poulton, Balch, Maranon, Adey et al., 2018; Mayers et al., this issue).

A component of the work also considered the role of the autumn bloom in the annual cycle of primary production (Wihsgott et al., this issue). The deepening autumnal surface mixed layer entrained nutrients at a time when there was sufficient light to drive photosynthesis. While the highest integrated chlorophyll concentrations were found associated with the spring bloom (~180 mg m⁻²), moderately high amounts were also found during the autumn bloom (~100 mg m⁻²), and estimates of carbon fixation rates during autumn were very close to rates calculated for the spring bloom (Wihsgott et al., this issue). Comparing the mooring-based estimates and the direct measurements of primary production rates (Poulton, Davis, Daniels, Mayers, Harris et al., this issue; Wihsgott et al., this issue) indicated that a high fraction (88%) of the autumnal primary production could be available for export. However, it was uncertain whether diatoms played a major role in autumn bloom primary production due to low light levels and high fractions of detrital biogenic silica leading to a dominance of dissolution on Si-cycling at this time (Poulton, Mayers, Daniels, Stinchcombe, Woodward et al., 2019).

The stoichiometry of carbon and nutrient uptake during key production periods varied significantly compared to Redfield. During the spring bloom in April 2015 phytoplankton uptake was found to be phosphorus-rich initially (early April) switching to carbon-rich in late
April, with some evidence that the dissolved organic phosphorus pool was utilized to support phosphorus requirements towards the end of the bloom (Poulton et al., this issue).

Subsequent primary production in the summer was found to be phosphorus-rich (Poulton et al., this issue), with the pool of dissolved organic matter (DOM) relatively carbon-rich (Davis, Blackbird, Wolff, Woodward & Mahaffey, this issue) due to retention of phosphorus and little release of dissolved organic phosphorus (Poulton et al., this issue). Measurements during the latter stages of an autumn bloom in November 2014 again showed carbon-rich uptake.

The overall indication through the entire sequence of cruises (spring, summer, autumn) suggested that production of DOM tended to be relatively carbon-rich compared to the uptake stoichiometry (Davis et al., this issue; Poulton et al., this issue).

The characteristics and potential sources of DOM were assessed over the full seasonal cycle. There was a strong and persistent cross-shelf gradient in terrigenous DOM, with about 24%, 36% and 43% of the winter dissolved organic carbon (DOC) at sites CD, CCS and CS2 respectively having a terrestrial origin (Carr, Davis, Blackbird, Daniels, Preece et al., this issue). At CCS this compares with the estimate for river-originated nitrate of 10% (Ruiz-Castillo et al., this issue). There was also a gradient in the molecular weight of the DOC, with higher molecular weight found closer to the terrestrial source. Release of DOC by phytoplankton at the CCS site was broadly consistent with bacterial demands (García-Martín, Daniels, Davidson, Davis, Mahaffey et al., this issue-a; García-Martín, Daniels, Davidson, Lozano, Mayers et al., this issue-b), while at the shelf edge site CS2 there was an influence from the open ocean (Carr et al., this issue). Largest concentrations of DOC were found in spring, and the lowest in autumn. The carbon content of the DOM pool was generally high, with the dissolved pool being carbon rich compared to both the particulate organic pool and Redfield (Davis et al., this issue). The majority (92-96%) of organic carbon was in the DOM pool throughout the sampling period, with a high C:N between 12 and 17.

The removal of organic carbon from the surface to deeper waters on the shelf varied through the year. In spring the downward flux was dominated by sinking particles (~8 mmol C m$^{-2}$...
day$^{-1}$), while in summer the diapycnal mixing of DOM into the bottom layer dominated the flux (~9 mmol C m$^{-2}$ day$^{-1}$) (Davis et al., this issue).

Further evidence towards determining the fate of the nutrient and carbon taken up by the phytoplankton is provided by measurements of phyto- and bacterio-plankton respiration (García-Martín et al., this issue-a; García-Martín et al., this issue-b). The plankton community was found to be net autotrophic in spring, suggesting organic carbon was available for higher trophic levels or for export, while in summer the plankton community had a more balanced metabolism. Importantly, the production of CO$_2$ by plankton respiration in surface waters was greater than the respiratory production of dissolved inorganic carbon (DIC) in deeper waters (García-Martín et al., this issue-a). Bacterial metabolism was never found to be limited by the availability of organic carbon, i.e. DOC production by phytoplankton was always sufficient to fuel bacterial carbon demand (García-Martín et al., this issue-a; García-Martín et al., this issue-b). The measured fluxes of DOM, and the general observation that the dissolved material tended to be carbon-rich, begins to point to the DOM as an important part of solving question (1) of the original research proposal. If the DOM can be exported to the open ocean, it will be taking excess carbon as a result of periods when phytoplankton uptake (and generation of DOM) was carbon-rich and also associated with the quicker remineralisation and recycling of the nitrogen and phosphorus in the DOM pool.

The dominance of nanoplankton in the spring bloom appeared to affect the grazing community, with larger microzooplankton (63-200 μm) attaining a higher trophic position than mesozooplankton (>500 μm) during this period (Giering et al., this issue). Overall, the Celtic Sea zooplankton community exhibited a close, positive coupling between biomass and trophic level. Estimated trophic levels increased through the spring bloom, apparently in response to higher primary production rates allowing greater numbers of predators. By contrast, the relatively high trophic levels observed during summer were attributed to the
predominance of a recycling-based community, with DOM-consuming bacteria supporting rapidly growing populations of flagellates and ciliates, which in turn provided a food source for omnivorous copepods. In autumn, the biomass and trophic level of the zooplankton community had declined, reflecting the dwindling availability of resources.

Size spectrum-derived estimates of zooplankton community trophic level were broadly consistent with those estimated using traditional stable isotope techniques, suggesting that size-based methods may offer a more holistic approach than focusing on a sub-set of numerically dominant species or taxa (Giering et al., this issue). However, contrasting explanations for the observed trophic levels in different seasons indicate that an overly simple size-based view of pelagic ecosystems, e.g. a given size-class feeds at a given trophic level, may be insufficient to capture the seasonal evolution of trophic interactions and their biogeochemical implications (Djeghri et al., this issue; Giering et al., this issue).

There were some significant contrasts between the zooplankton communities of the shelf (CCS) and shelf-edge (CS2) stations, with the latter likely controlled by the predatory activities of macrozooplankton and planktivorous fish (Giering et al., this issue). This is consistent with the known role of the shelf edge in supporting key spawning stocks of commercial fish species (Reid, 2001; Sharples, Moore, Hickman, Holligan, Tweddle et al., 2009). Monthly changes in copepod diet and prey preferences were determined over a year, taking advantage of the regular visits to the L4 and E1 stations as a part of the Western Channel Observatory. The five species of copepod investigated typically displayed unselective feeding behaviour, with the composition of their diet reflecting that of the available food. Some evidence for positive selection of motile prey was apparent, but there was no consistency in copepod feeding traits responding to changes in the dominant food type (Djeghri et al., this issue). Considerable plasticity in the ratio between the sizes of copepods and their food across the seasonal cycle challenges the validity of parameterizing zooplankton feeding in size-based models using a unimodal function.
On the scale of the entire northwest European shelf, and consistent with published studies on the North Sea (Thomas, Bozec, de Baar, Elkalay, Frankignoule et al., 2005) and the Celtic Sea (Marrec et al., 2015), seasonally-stratified areas of the shelf showed a net deficit in pCO$_2$ compared to the atmosphere, indicating net carbon drawdown from the atmosphere to the sea (Hartman et al., this issue) and implying subsequent export off the shelf. Mixed regions, such as the central and eastern English Channel and the southern North Sea, showed significant excesses in pCO$_2$ compared to the atmosphere, indicating a net source of carbon to the atmosphere over one year. The intensive field programme in the Celtic Sea delivered a high resolution description of the seasonal cycle in the carbonate system. Surface water pCO$_2$ was close to, or slightly below, atmospheric pCO$_2$, with the net annual drawdown being driven mainly by a significant biologically-driven pCO$_2$ deficit in spring (Hartman et al., this issue).

Nitrate:phosphate in surface waters was almost always less than Redfield indicating a generally nitrogen limited system, whilst DIC:nitrate varied throughout the year from low values in winter and early spring when nitrate was in abundance, to values greater than Redfield as phytoplankton productivity depleted available nitrate. (Humphreys et al., this issue) considered the details of the Celtic Sea carbonate system using the sampling at the CCS site. They found that over 1.5 mol C m$^{-2}$, or >50%, of the annual net community production at CCS was stored in recalcitrant organic matter with a lifetime of at least several months. They also calculated the net air-sea drawdown of carbon at CCS to be about 1.3 mol C m$^{-2}$, suggesting that a carbon-rich recalcitrant DOM pool could be a key part of supporting carbon export while allowing the shelf to retain nutrients. A build-up of high DIC in shelf bottom waters, combined with annual flushing, could support carbon export (e.g. as suggested for the North Sea (Thomas, Bozec, Elkalay & de Baar, 2004)). A mismatch was observed between the DIC and nutrients between March 2014 (when concentrations were similar to those in the adjacent open Atlantic Ocean) and March 2015 (reduced nutrients and
slightly increased DIC). This mismatch indicates that flushing of the shelf water is not an annual occurrence, and so an alternative export mechanism was suggested: long-lived carbon-rich DOM could function as an export route, storing carbon on the shelf long enough for episodic large-scale physically-driven exchange events to remove the carbon build-up to the adjacent Atlantic Ocean.

4. Implications for Shelf Nutrient Supply and Carbon Export.

A role for DOC in carbon export in the open ocean and shelf seas is well-established (Barron & Duarte, 2015; Chaichana, Jickells & Johnson, 2019; Hopkinson & Vallino, 2005; Hopkinson, Vallino & Nolin, 2002). Our view emerging from the Shelf Sea Biogeochemistry research programme is that the export of carbon from the wide northwest European shelf is strongly dependent on the ability of the recalcitrant organic matter pool to store carbon on the shelf, maintaining a net air-sea drawdown of CO$_2$ with episodic flushing events eventually removing this carbon into the open Atlantic Ocean. We have found that the shelf sea accumulates carbon-rich organic matter as a result of carbon-rich uptake by phytoplankton following seasonal nutrient reduction, and preferential remineralisation and recycling of organic nitrogen and phosphorus. The episodic nature of the exchange events with the open ocean was inferred from the change in the carbon and nutrient characteristics across 12 months (Humphreys et al., this issue) suggesting that re-setting the carbon and nutrient pools with oceanic water does not happen every year. This idea of episodic exchange is consistent with our observations of physical transports and the potential for exchange with the open ocean. Within the 12 months of sampling we did see some transport of shelf water towards the shelf edge during winter, but based on the changes in outer shelf salinities it appears that only the outer ~100 km of the shelf sea gained access to the shelf edge for any possible exchange with the ocean (Ruiz-Castillo et al., this issue). However, at the same time our results showed that the entire seasonally-stratifying Celtic Sea achieved a net annual air-sea drawdown of CO$_2$ (Hartman et al., this issue). Thus, while the air-sea flux suggests wide-scale carbon export, the physical transports were insufficient to export all of
the carbon-laden water: storage in a recalcitrant pool of carbon-rich DOM provides a mechanism for holding the carbon on the shelf between exchange events.

While episodic exchange of a gradually increasing pool of refractory organic carbon solves the carbon export problem, at the same time the shelf needs to hold on to nutrients to fuel the primary production (and the DOC production). The carbon export events will also be responsible for replenishing the shelf nutrient pool from the ocean, with our estimate at the CCS site being that 90% of the inorganic nitrate was of oceanic origin. Nitrate flux from the shelf edge was observed (Ruiz-Castillo et al., this issue) but our nitrate budget suggests that only about 25% of the March 2015 nitrate pool was of recent oceanic origin; recycling of organic nitrogen on the shelf accounts for 50-62% of the March 2015 nitrate pool. The remaining nitrate found in March 2015 was either unused from the previous year or has a riverine origin.

Our suggested answer to the conundrum of how a wide shelf sea manages to export carbon while maintaining a pool of nutrients is, therefore, a combination of carbon storage in the recalcitrant DOC pool, coupled with efficient recycling and retention of nitrogen and phosphorus, and episodic exchange events with the NE Atlantic Ocean to finally remove the carbon and to replenish lost nutrients. Annual variation in dissolved organic carbon concentrations, which would arise from episodic exchange, has recently been shown in the North Sea (Chaichana et al., 2019). Key questions that now need to be addressed are on the relative roles of prokaryotic and eukaryotic organisms in driving the breakdown and recycling of material, and on the mechanisms and frequency of physical exchange processes between the shelf and the open ocean.

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