

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

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23 **Abstract.**

24 This special issue presents some of the key findings from the pelagic component of the UK
25 Shelf Sea Biogeochemistry Research Programme, carried out on the northwest European
26 shelf between March 2014 and August 2015. The project aimed to address two issues: (1)
27 how does a temperate shelf sea sustain an annual net drawdown and export of atmospheric
28 CO₂ without running out of inorganic nutrients, and (2) what uncertainties in processes or
29 parameterisations within current ecosystem models can be reduced by a coordinated, multi-
30 disciplinary observational programme covering the full seasonal cycle? Working with
31 partners across Europe, the net annual drawdown of atmospheric CO₂ over the entire
32 northwest European shelf was confirmed. This demonstrated the context and impetus for a
33 17-month process study in the Celtic Sea, using a long-term mooring array and several
34 research cruises, addressing shelf sea physics, inorganic and organic nutrient and carbon
35 cycling, and bacterial, phytoplankton and zooplankton roles and dynamics. It was clear from
36 the physics that all the carbon absorbed through the sea surface over one year was not
37 exported to the open ocean. Physical transports were too weak and too slow to transport all
38 the carbon-laden water over a wide shelf sea to the shelf edge within one year. The shelf
39 sea must therefore be able to store carbon in a form that prevents release back to the
40 atmosphere for a timescale that is sufficient to allow more episodic (timescales > 1 year)
41 exchange events to both remove the excess carbon and top-up the shelf pool of inorganic
42 nutrients. The results presented in this special issue illustrate the likely key role of
43 recalcitrant dissolved organic carbon in storing carbon on the shelf and highlight the need for
44 longer-term measurements or monitoring to understand the nature and timing of potentially
45 large but infrequent exchange events between the shelf and open ocean.

46

47 **1. Introduction.**

48 Shelf seas play a significant role in the global cycling of carbon by the oceans, driving
49 between 10 and 30% of marine primary production, 30 to 50% of inorganic carbon burial and
50 ~80% of organic carbon burial (Bauer, Cai, Raymond, Bianchi, Hopkinson et al., 2013; Liu,

51 Atkinson, Quinones & Talaue-McManus, 2010; Mackenzie, Andersson, Lerman & Ver,
52 2005). Overall, the present-day shelf seas are a net sink for atmospheric CO₂, though this
53 may be a relatively new phenomenon: pre-industrial shelf seas are likely to have been a net
54 source of CO₂ to the atmosphere, with the switch to a net sink occurring as a response to
55 anthropogenic increases in atmospheric CO₂ (Bauer et al., 2013; Laruelle, Cai, Hu, Gruber,
56 Mackenzie et al., 2018; Mackenzie, Lerman & Andersson, 2004). Thus, shelf seas play a
57 disproportionately important role in global carbon cycling and Earth's climate relative to their
58 limited geographical area, with their current role a response to anthropogenic forcing.

59

60 Shelf seas also provide a range of services to the increasing human populations which live
61 and work in coastal areas. They make a vital contribution to the food supplies required by
62 the global human population, with more than 90% of global fish catches taken from shelf
63 seas (Pauly, Christensen, Guenette, Pitcher, Sumaila et al., 2002). These shallow, coastal
64 seas receive material delivered by river run-off, often including high loads of sediments,
65 nutrients and carbon (Beusen, Dekkers, Bouwman, Ludwig & Harrison, 2005; Seitzinger,
66 Mayorga, Bouwman, Kroeze, Beusen et al., 2010). The shelf seas act as a buffer between
67 rivers and the open ocean, processing river-borne material and reducing the amount that
68 reaches beyond the shelf edge (Izett & Fennel, 2018; Painter, Lapworth, Woodward,
69 Kroeger, Evans et al., 2018; Sharples, Middelburg, Fennel & Jickells, 2017). The type and
70 amount of material that is carried by rivers is sensitive to the human management of
71 catchment areas (Bouwman, Beusen & Billen, 2009) and the extent of wastewater treatment
72 (Van Drecht, Bouwman, Harrison & Knoop, 2009). High nutrient loading arising from
73 agricultural run-off and wastewater release often results in enhanced biological oxygen
74 demand and reduced dissolved oxygen concentrations, to the detriment of coastal
75 ecosystems and fisheries (Diaz & Rosenberg, 2008; Fennel & Testa, 2019; Rabalais, Diaz,
76 Levin, Turner, Gilbert et al., 2010).

77

78 It is this combined background of the shelf seas' central role in the global carbon cycle and
79 climate, the importance of shelf seas to food supply and waste dispersal, and the changes to
80 these roles in response to future human activities that led to the development of the UK
81 Shelf Sea Biogeochemistry research programme, funded through the UK Natural
82 Environment Research Council (NERC) and the UK government Department of Environment
83 Food and Rural Affairs (Defra). As well as water column physics, biology and
84 biogeochemistry, the programme included observational components on sediment
85 biogeochemistry (e.g. (Hicks, Ubbara, Silburn, Smith, Kroger et al., 2017; Kitidis, Tait,
86 Nunes, Brown, Woodward et al., 2017; Thompson, Silburn, Williams, Hull, Sivyer et al.,
87 2017)), iron cycling (e.g. (Birchill, Milne, Woodward, Harris, Annett et al., 2017)) and
88 ecosystem modelling (e.g. (Butenschoen, Clark, Aldridge, Allen, Artioli et al., 2016)).

89

90 The papers presented in this Special Issue arise from detailed observational studies of
91 pelagic physics and biogeochemistry across the Celtic Sea on the northwest European
92 continental shelf (Fig. 1), an archetypal temperate shelf environment that undergoes
93 seasonal stratification with distinct spring and autumn plankton blooms (Sharples & Holligan,
94 2006). The project began with two overarching questions:

95 (1) **How can a shelf sea export carbon to the open ocean without running out of**
96 **nutrients?** This question arises from a thought experiment of what happens to the
97 nutrients on a shelf if biogeochemical cycling operates with a fixed stoichiometry of
98 carbon to nitrogen to phosphorus (here we assume the Redfield ratio C:N:P of
99 106:16:1 (Redfield, 1934)). Carbon exported to the open ocean (with its concomitant
100 N and P) is replaced via a CO₂ influx from the atmosphere. There then needs to be
101 one or more processes that fulfill the same role for nutrients, replacing the exported
102 nutrients and allowing the shelf system to continue operating with a fixed
103 stoichiometry. The focus for this excess nutrient supply was on one or more of: non-
104 Redfield carbon uptake (e.g. (Bozec, Thomas, Schiettecatte, Borges, Elkalay et al.,
105 2006)); preferential recycling and shelf retention of nutrients (e.g. (Lonborg,

106 Davidson, Alvarez-Salgado & Miller, 2009; Toggweiler, 1993)) compared to carbon
107 on the shelf; and excess nutrient delivery from rivers (e.g. (Jickells, 1998)) (if we
108 assume that delivery from the ocean occurs with the same stoichiometry as the
109 biogeochemical cycling on the shelf).

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

117

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

123

124 **2. The Observational Programme.**

125 The broader geographical focus of the Shelf Sea Biogeochemistry programme was on the
126 wide continental shelf areas of northwest Europe, with a process-study focus on the Celtic
127 Sea (Fig. 1). Seasonally stratifying parts of the shelf (the Celtic Sea and western English
128 Channel, the northern North Sea and the Malin Sea, Fig. 1) are net annual sinks for
129 atmospheric CO₂. About 6×10^{12} mol C are exported to the adjacent northeast Atlantic
130 Ocean, about half of which may be transported below the seasonal pycnocline off the shelf
131 (Borges, Schiettecatte, Abril, Delille & Gazeau, 2006; Wakelin, Holt, Blackford, Allen,
132 Butenschon et al., 2012). At the scale of the entire northwest European shelf the aim of the
133 project was, via extensive collaborations with other European partners, to assess the net

134 annual air-sea flux of CO₂ alongside the surface ocean biogeochemistry. The Celtic Sea
135 contributes to this overall shelf carbon export (Marrec, Cariou, Mace, Morin, Salt et al., 2015)
136 and was chosen for the focus of the process studies as it enables the full (seasonal) range of
137 shelf processes and environments to be easily reachable over a typical 30 day research
138 cruise.

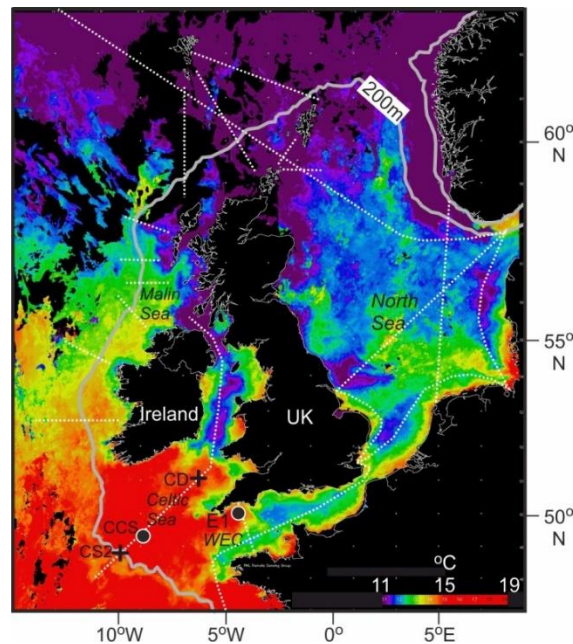


Figure 1.

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 (Djehri, 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.

139

140 The field programme began in March 2014, with the deployment of an array of moorings at
141 the Central Celtic Sea (CCS) site (Fig. 1). CCS was situated in the middle of the seasonally-
142 stratifying region, about 100 km from the shelf edge and clear of significant fishing activity
143 (e.g. (Sharples, Ellis, Nolan & Scott, 2013)). The moorings provided a total of 17 months of
144 almost continuous data on water column physical structure (temperature, salinity and
145 currents), surface chlorophyll (fluorescence) and nutrients (a Smartbuoy operated by the
146 Centre for Environment Fisheries and Aquaculture Science) and meteorology (operated by
147 the UK Meteorological Office). Station CS2 was an established study site at the shelf edge,
148 where mixing by a breaking internal tide is a key underpinning physical process
149 (e.g.(Sharples, Tweddle, Green, Palmer, Kim et al., 2007)). Station CD (Celtic Deep) was a
150 joint station operated by the pelagic and benthic components of the Shelf Sea
151 Biogeochemistry research programme, and the long-term mooring at E1 provided additional
152 time series in a shallower seasonally-stratifying location. Stations CCS, CS2 and CD were
153 visited several times during each of the pelagic process study cruises; a basic suite of
154 information was collected at CCS and CS2 during cruises operated by the benthic project;
155 station CD was the main process study site for the benthic project and marked the
156 northernmost sampling site for the pelagic process study cruises. A total of 9 research
157 cruises were carried out between March 2014 and August 2015, with the main pelagic
158 process study cruises occurring in November 2014, April 2015 and July 2015.

159

160 **3. Summary of Key Results.**

161 (Ruiz-Castillo, Sharples, Hopkins & Woodward, this issue) illustrate the underpinning
162 changes in the cross-shelf physical structure, using the CTD transect data from all available
163 cruises. As expected, the shelf stratified in April (2014 and 2015), with stratification then
164 maintained until late December. The salinity distributions from the CTD transects are used to
165 assess the likely rates of horizontal transport across the shelf. Movement of higher salinity
166 water from the shelf edge in towards the shelf interior in summer suggested a mechanism for

167 the supply of oceanic nutrients, largely a result of wind-driven flows but with a significant
168 contribution from Stoke's drift associated with internal tidal waves. There was a clear
169 indication of cross-shelf transport towards the shelf edge in winter, with the outer 100 km of
170 shelf water potentially reaching the shelf edge to be exchanged with the open ocean. The
171 mean transport of about $1 \text{ m}^2 \text{ s}^{-1}$ was a combination of wind-driven transport and an
172 estuarine-like flow driven by the horizontal density gradient caused by differential cooling as
173 the shelf shallowed. (Ruiz-Castillo et al., this issue) also attempted a basic seasonal budget
174 of nitrate at the CCS mooring site, taking into account cross-shelf transports, an estimate of
175 riverine contribution, vertical mixing across the seasonal pycnocline, and uptake during the
176 spring and autumn blooms and within the summer sub-surface chlorophyll layer. Comparing
177 the nitrate available in March 2014 with that found in March 2015, the implication was that
178 50-62% of the available nitrate in March 2015 was locally recycled (consistent with tight
179 coupling observed within the plankton community (Giering, Wells, Mayers, Schuster,
180 Cornwell et al., this issue)), with the remaining 38-50% either (in descending order) unused
181 during the previous 12 months, supplied via transport from the shelf edge, or contributed by
182 rivers. The latter was estimated to be about 10% of the available nitrate at CCS.

183

184 High-resolution oxygen measurements during the spring bloom showed large changes in
185 rates of net community production occurring within just a few hours. The fraction of primary
186 production on the shelf estimated to be available for export (based on net and gross
187 community oxygen production) was found to be 0.25, compared to 0.07 off the edge of the
188 shelf, indicating the importance of primary production on the wide, shallow shelf for carbon
189 export (Seguro, Marca, Painting, Shutler, Suggett et al., this issue). It was found, however,
190 that the phytoplankton community in the spring bloom was made up of nanoplankton (2-20
191 μm), which differed from expectations of larger spring bloom phytoplankton (i.e. large
192 diatoms) based on earlier work (e.g. (Rees, Joint & Donald, 1999)) potentially lowering the
193 export fraction in April 2015. Calcite production by coccolithophores during the spring bloom
194 was measured to determine the contribution to total bloom carbon fixation that might counter

195 biological drawdown of inorganic carbon. Only 0.2 to 2% of spring bloom primary production
196 was found to be carried out by the coccolithophores, with strong top-down control on
197 coccolithophore growth as microzooplankton (20-200 μm) removed about 60% of daily
198 calcite production (Mayers, Poulton, Daniels, Wells, Woodward et al., this issue), though the
199 fate of this grazed material (internal dissolution or packaging into fecal pellets) was
200 unknown. An exception to this was a single site in the northern Celtic Sea, where a marked
201 bloom (>2000 cells mL^{-1}) of *Emiliana huxleyi* accounted for 30% of the total primary
202 production and led to some of the highest reported calcite production rates in the ocean
203 (Daniels, Poulton, Balch, Maranon, Adey et al., 2018; Mayers et al., this issue).

204

205 A component of the work also considered the role of the autumn bloom in the annual cycle of
206 primary production (Wihsgott et al., this issue). The deepening autumnal surface mixed layer
207 entrained nutrients at a time when there was sufficient light to drive photosynthesis. While
208 the highest integrated chlorophyll concentrations were found associated with the spring
209 bloom (~ 180 mg m^{-2}), moderately high amounts were also found during the autumn bloom
210 (~ 100 mg m^{-2}), and estimates of carbon fixation rates during autumn were very close to rates
211 calculated for the spring bloom (Wihsgott et al., this issue). Comparing the mooring-based
212 estimates and the direct measurements of primary production rates (Poulton, Davis, Daniels,
213 Mayers, Harris et al., this issue; Wihsgott et al., this issue) indicated that a high fraction
214 (88%) of the autumnal primary production could be available for export. However, it was
215 uncertain whether diatoms played a major role in autumn bloom primary production due to
216 low light levels and high fractions of detrital biogenic silica leading to a dominance of
217 dissolution on Si-cycling at this time (Poulton, Mayers, Daniels, Stinchcombe, Woodward et
218 al., 2019).

219

220 The stoichiometry of carbon and nutrient uptake during key production periods varied
221 significantly compared to Redfield. During the spring bloom in April 2015 phytoplankton
222 uptake was found to be phosphorus-rich initially (early April) switching to carbon-rich in late

223 April, with some evidence that the dissolved organic phosphorus pool was utilized to support
224 phosphorus requirements towards the end of the bloom (Poulton et al., this issue).
225 Subsequent primary production in the summer was found to be phosphorus-rich (Poulton et
226 al., this issue), with the pool of dissolved organic matter (DOM) relatively carbon-rich (Davis,
227 Blackbird, Wolff, Woodward & Mahaffey, this issue) due to retention of phosphorus and little
228 release of dissolved organic phosphorus (Poulton et al., this issue). Measurements during
229 the latter stages of an autumn bloom in November 2014 again showed carbon-rich uptake.
230 The overall indication through the entire sequence of cruises (spring, summer, autumn)
231 suggested that production of DOM tended to be relatively carbon-rich compared to the
232 uptake stoichiometry (Davis et al., this issue; Poulton et al., this issue).

233

234 The characteristics and potential sources of DOM were assessed over the full seasonal
235 cycle. There was a strong and persistent cross-shelf gradient in terrigenous DOM, with about
236 24%, 36% and 43% of the winter dissolved organic carbon (DOC) at sites CD, CCS and CS2
237 respectively having a terrestrial origin (Carr, Davis, Blackbird, Daniels, Preece et al., this
238 issue). At CCS this compares with the estimate for river-originated nitrate of 10% (Ruiz-
239 Castillo et al., this issue). There was also a gradient in the molecular weight of the DOC, with
240 higher molecular weight found closer to the terrestrial source. Release of DOC by
241 phytoplankton at the CCS site was broadly consistent with bacterial demands (García-
242 Martín, Daniels, Davidson, Davis, Mahaffey et al., this issue-a; García-Martín, Daniels,
243 Davidson, Lozano, Mayers et al., this issue-b), while at the shelf edge site CS2 there was an
244 influence from the open ocean (Carr et al., this issue). Largest concentrations of DOC were
245 found in spring, and the lowest in autumn. The carbon content of the DOM pool was
246 generally high, with the dissolved pool being carbon rich compared to both the particulate
247 organic pool and Redfield (Davis et al., this issue). The majority (92-96%) of organic carbon
248 was in the DOM pool throughout the sampling period, with a high C:N between 12 and 17.
249 The removal of organic carbon from the surface to deeper waters on the shelf varied through
250 the year. In spring the downward flux was dominated by sinking particles ($\sim 8 \text{ mmol C m}^{-2}$

251 day⁻¹), while in summer the diapycnal mixing of DOM into the bottom layer dominated the
252 flux (~9 mmol C m⁻² day⁻¹) (Davis et al., this issue).

253

254 Further evidence towards determining the fate of the nutrient and carbon taken up by the
255 phytoplankton is provided by measurements of phyto- and bacterio-plankton respiration
256 (García-Martín et al., this issue-a; García-Martín et al., this issue-b). The plankton
257 community was found to be net autotrophic in spring, suggesting organic carbon was
258 available for higher trophic levels or for export, while in summer the plankton community had
259 a more balanced metabolism. Importantly, the production of CO₂ by plankton respiration in
260 surface waters was greater than the respiratory production of dissolved inorganic carbon
261 (DIC) in deeper waters (García-Martín et al., this issue-a). Bacterial metabolism was never
262 found to be limited by the availability of organic carbon, i.e. DOC production by
263 phytoplankton was always sufficient to fuel bacterial carbon demand (García-Martín et al.,
264 this issue-a; García-Martín et al., this issue-b). The measured fluxes of DOM, and the
265 general observation that the dissolved material tended to be carbon-rich, begins to point to
266 the DOM as an important part of solving question (1) of the original research proposal. If the
267 DOM can be exported to the open ocean, it will be taking excess carbon as a result of
268 periods when phytoplankton uptake (and generation of DOM) was carbon-rich and also
269 associated with the quicker remineralisation and recycling of the nitrogen and phosphorus in
270 the DOM pool.

271

272 The dominance of nanoplankton in the spring bloom appeared to affect the grazing
273 community, with larger microzooplankton (63-200 µm) attaining a higher trophic position
274 than mesozooplankton (>500 µm) during this period (Giering et al., this issue). Overall, the
275 Celtic Sea zooplankton community exhibited a close, positive coupling between biomass and
276 trophic level. Estimated trophic levels increased through the spring bloom, apparently in
277 response to higher primary production rates allowing greater numbers of predators. By
278 contrast, the relatively high trophic levels observed during summer were attributed to the

279 predominance of a recycling-based community, with DOM-consuming bacteria supporting
280 rapidly growing populations of flagellates and ciliates, which in turn provided a food source
281 for omnivorous copepods. In autumn, the biomass and trophic level of the zooplankton
282 community had declined, reflecting the dwindling availability of resources.

283

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

292

293 There were some significant contrasts between the zooplankton communities of the shelf
294 (CCS) and shelf-edge (CS2) stations, with the latter likely controlled by the predatory
295 activities of macrozooplankton and planktivorous fish (Giering et al., this issue). This is
296 consistent with the known role of the shelf edge in supporting key spawning stocks of
297 commercial fish species (Reid, 2001; Sharples, Moore, Hickman, Holligan, Tweddle et al.,
298 2009). Monthly changes in copepod diet and prey preferences were determined over a year,
299 taking advantage of the regular visits to the L4 and E1 stations as a part of the Western
300 Channel Observatory. The five species of copepod investigated typically displayed
301 unselective feeding behaviour, with the composition of their diet reflecting that of the
302 available food. Some evidence for positive selection of motile prey was apparent, but there
303 was no consistency in copepod feeding traits responding to changes in the dominant food
304 type (Djehgri et al., this issue). Considerable plasticity in the ratio between the sizes of
305 copepods and their food across the seasonal cycle challenges the validity of parameterizing
306 zooplankton feeding in size-based models using a unimodal function.

307

308 On the scale of the entire northwest European shelf, and consistent with published studies
309 on the North Sea (Thomas, Bozec, de Baar, Elkalay, Frankignoulle et al., 2005) and the
310 Celtic Sea (Marrec et al., 2015), seasonally-stratified areas of the shelf showed a net deficit
311 in pCO₂ compared to the atmosphere, indicating net carbon drawdown from the atmosphere
312 to the sea (Hartman et al., this issue) and implying subsequent export off the shelf. Mixed
313 regions, such as the central and eastern English Channel and the southern North Sea,
314 showed significant excesses in pCO₂ compared to the atmosphere, indicating a net source
315 of carbon to the atmosphere over one year. The intensive field programme in the Celtic Sea
316 delivered a high resolution description of the seasonal cycle in the carbonate system.
317 Surface water pCO₂ was close to, or slightly below, atmospheric pCO₂, with the net annual
318 drawdown being driven mainly by a significant biologically-driven pCO₂ deficit in spring
319 (Hartman et al., this issue).

320

321 Nitrate:phosphate in surface waters was almost always less than Redfield indicating a
322 generally nitrogen limited system, whilst DIC:nitrate varied throughout the year from low
323 values in winter and early spring when nitrate was in abundance, to values greater than
324 Redfield as phytoplankton productivity depleted available nitrate. (Humphreys et al., this
325 issue) considered the details of the Celtic Sea carbonate system using the sampling at the
326 CCS site. They found that over 1.5 mol C m⁻², or >50%, of the annual net community
327 production at CCS was stored in recalcitrant organic matter with a lifetime of at least several
328 months. They also calculated the net air-sea drawdown of carbon at CCS to be about 1.3
329 mol C m⁻², suggesting that a carbon-rich recalcitrant DOM pool could be a key part of
330 supporting carbon export while allowing the shelf to retain nutrients. A build-up of high DIC in
331 shelf bottom waters, combined with annual flushing, could support carbon export (e.g. as
332 suggested for the North Sea (Thomas, Bozec, Elkalay & de Baar, 2004)). A mismatch was
333 observed between the DIC and nutrients between March 2014 (when concentrations were
334 similar to those in the adjacent open Atlantic Ocean) and March 2015 (reduced nutrients and

335 slightly increased DIC). This mismatch indicates that flushing of the shelf water is not an
336 annual occurrence, and so an alternative export mechanism was suggested: long-lived
337 carbon-rich DOM could function as an export route, storing carbon on the shelf long enough
338 for episodic large-scale physically-driven exchange events to remove the carbon build-up to
339 the adjacent Atlantic Ocean.

340

341 **4. Implications for Shelf Nutrient Supply and Carbon Export.**

342 A role for DOC in carbon export in the open ocean and shelf seas is well-established (Barron
343 & Duarte, 2015; Chaichana, Jickells & Johnson, 2019; Hopkinson & Vallino, 2005;
344 Hopkinson, Vallino & Nolin, 2002). Our view emerging from the Shelf Sea Biogeochemistry
345 research programme is that the export of carbon from the wide northwest European shelf is
346 strongly dependent on the ability of the recalcitrant organic matter pool to store carbon on
347 the shelf, maintaining a net air-sea drawdown of CO₂ with episodic flushing events
348 eventually removing this carbon into the open Atlantic Ocean. We have found that the shelf
349 sea accumulates carbon-rich organic matter as a result of carbon-rich uptake by
350 phytoplankton following seasonal nutrient reduction, and preferential remineralisation and
351 recycling of organic nitrogen and phosphorus. The episodic nature of the exchange events
352 with the open ocean was inferred from the change in the carbon and nutrient characteristics
353 across 12 months (Humphreys et al., this issue) suggesting that re-setting the carbon and
354 nutrient pools with oceanic water does not happen every year. This idea of episodic
355 exchange is consistent with our observations of physical transports and the potential for
356 exchange with the open ocean. Within the 12 months of sampling we did see some transport
357 of shelf water towards the shelf edge during winter, but based on the changes in outer shelf
358 salinities it appears that only the outer ~100 km of the shelf sea gained access to the shelf
359 edge for any possible exchange with the ocean (Ruiz-Castillo et al., this issue). However, at
360 the same time our results showed that the entire seasonally-stratifying Celtic Sea achieved a
361 net annual air-sea drawdown of CO₂ (Hartman et al., this issue). Thus, while the air-sea flux
362 suggests wide-scale carbon export, the physical transports were insufficient to export all of

363 the carbon-laden water: storage in a recalcitrant pool of carbon-rich DOM provides a
364 mechanism for holding the carbon on the shelf between exchange events.

365

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

376

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

387

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