Controls over Ocean Mesopelagic Interior Carbon Storage (COMICS): fieldwork, synthesis and modelling efforts

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31 **Abstract**

32 The ocean's biological carbon pump plays a central role in regulating atmospheric CO_2
33 levels. In particular, the depth at which sinking organic carbon is broken down and respired
34 in the mesopelagic zone is critical, with deeper remineralisation resulting in greater carbon
35 storage. Until recently, however, a balanced budget of the supply and consumption of organic
36 carbon in the mesopelagic had not been constructed in any region of the ocean, and the
37 processes controlling organic carbon turnover are still poorly understood. Large-scale data
38 syntheses suggest that a wide range of factors can influence remineralisation depth including
39 upper-ocean ecological interactions, and interior dissolved oxygen concentration and
40 temperature. However these analyses do not provide a mechanistic understanding of
41 remineralisation, which increases the challenge of appropriately modelling the mesopelagic
42 carbon dynamics. In light of this, the UK Natural Environment Research Council has funded
43 a programme with this mechanistic understanding as its aim, drawing targeted fieldwork right
44 through to implementation of a new parameterisation for mesopelagic remineralisation within
45 an IPCC class global biogeochemical model. The Controls over Ocean Mesopelagic Interior
46 Carbon Storage (COMICS) programme will deliver new insights into the processes of carbon
47 cycling in the mesopelagic zone and how these influence ocean carbon storage. Here we
48 outline the programme's rationale, its goals, planned fieldwork and modelling activities, with
49 the aim of stimulating international collaboration.

50

51

52 **Motivation**

53 The oceanic production, export to depth and remineralisation of organic carbon consitutes the
54 biological carbon pump, the suite of processes that currently store enough carbon in the
55 ocean's interior to keep atmospheric CO_2 200 ppm lower than it would otherwise be (Parekh
56 et al., 2006). The size of this stored carbon pool is dictated by the sinking flux of organic
57 carbon into the ocean interior and its residence time in the deep ocean, which is a function of
58 the depth at which sinking carbon is remineralised (Kwon et al., 2009), with deeper
59 remineralisation leading to increased storage.

60

61 Multiple mechanisms contribute to the flux of organic matter to the ocean interior. The
62 majority of studies focus on sinking particles, such as faecal pellets, marine snow aggregates
63 and individual organisms. Faecal pellets play a significant role at some times of the year, with
64 their flux to the seafloor on occasions representing up to 70% of the total flux (Manno et al.,
65 2015). Aggregates can also contribute large fluxes, especially in the aftermath of diatom
66 blooms (e.g. Martin et al., 2011). The assumption is often made, based on Bishop et al.
67 (1977), that the bulk of the flux is carried by large, rapidly sinking aggregates. However
68 recent observations (Alonso-Gonzalez et al., 2010; Riley et al., 2012; Villa-Alfageme et al.,
69 2014) suggest that, on occasion, a significant fraction of flux sinks much more slowly. Our
70 understanding of this slow sinking fraction is in its infancy, although a model study suggests
71 that its importance may be widespread, with knowledge of its variability key to understanding
72 what fraction of primary production is exported, i.e. the export efficiency (Henson et al.,
73 2015).

74

75   A range of other processes also transfer organic carbon into the ocean interior including
76   advection and mixing of dissolved organic carbon (DOC), diel vertical migration (DVM) of
77   zooplankton, and production by chemosynthesis. Whilst DOC transport is a surface
78   intensified process, chemosynthesis and DVM have the potential to directly supply organic
79   carbon to deeper waters. DOC transport can form a significant (~ 50%) fraction of total
80   export flux in the oligotrophic subtropical gyres (Carlson et al., 2010; Pan et al., 2014).
81   During DVM, zooplankton swim to the surface at night to feed and then return to depth
82   during the day where they respire and egest some of the material they have ingested at the
83   surface and release some of it as DOC and particulate organic carbon (POC). This is the so
84   called 'active flux' which can be a significant term in mesopelagic carbon budgets
85   (equivalent to 2-40% of the gravitational POC flux at 150 m; Steinberg et al., 2008; Giering
86   et al. 2014). Chemosynthesis - new production by chemolithotrophic bacteria and archaea,
87   which may be enhanced in anoxic regions (Juniper and Brinkhurst, 1986) - uses reduced
88   inorganic substrates (e.g. sulphides and ammonia) as an energy source and CO_2 as a carbon
89   source. Chemosynthesis may significantly contribute to the mesopelagic carbon budget
90   (Alonso-Saez et al., 2010; Herndl and Reinthaler 2013), with rates of chemoautotrophic CO_2
91   fixation comparable to heterotrophic production (Reinthaler et al., 2010).

92

93   Because of the complexity and multitude of processes contributing to export flux and
94   remineralisation, closing the mesopelagic carbon budget has proved challenging until
95   recently, with estimates of organic carbon sources and sinks differing by up to an order of
96   magnitude (Steinberg et al., 2008; Burd et al., 2010). However, in 2014, the first balanced
97   oceanic mesopelagic carbon budget was published for the Northeast Atlantic Ocean (Giering
98   et al., 2014, hereafter G14). A key result of G14 was that, whereas both zooplankton and
99   microbes consume sinking particles in approximately equal measure, the zooplankton serve
100 primarily to fragment this material. It is possible that this fragmentation increases the
101 material's nutritive value by promoting the growth of microbes (Mayor et al., 2014). G14
102 demonstrated that a consequence of the fragmentation is that respiration by prokaryotes is the
103 dominant sink for organic carbon.

104

105 Whilst G14 demonstrated that we now have the tools to understand and measure mesopelagic
106 processes, it only considered a single site in the North Atlantic and only balanced the budget
107 over the entire mesopelagic zone, probably due to inadequate representation of DVM or to
108 uncertainties associated with the calculation of bacterial respiration. Given this state of the
109 research field, we identify the following priorities for biological carbon pump research:

110 1) To achieve a mechanistic understanding of the key processes in, and overall function of,
111   the mesopelagic system;

112 2) To close the budget (carbon supply versus carbon demand) at other, contrasting locations;

113 3) To balance the budget in discrete layers within the mesopelagic to identify the vertical
114   phasing and interplay of processes;

115 4) To represent mesopelagic remineralisation dynamically in IPCC class models in order to
116   improve simulations of ocean carbon storage.

117

118 **Controls on mesopelagic remineralisation**

119 Most efforts to understand the large scale controls on interior remineralisation have focussed
120 on the sinking flux, quantifying its loss via the transfer efficiency (TE; flux at depth relative
121 to flux at the base of the mixed layer), calculated from surface observations and deep trap
122 flux data. Francois et al. (2002) and Henson et al. (2012) both suggest that TE is low at high
123 latitudes and high at low latitudes. They explain this pattern in terms of surface biological
124 properties, suggesting that highly productive communities, typically found in cool regions,
125 have low surface recycling rates, but also low TE due to the sinking of highly labile
126 aggregates which are remineralised efficiently in the mesopelagic. In contrast, communities
127 residing in warm oligotrophic waters, have high values of TE due to high levels of surface
128 recycling and the production of refractory aggregates. This picture is further complicated by
129 the ballast hypothesis (Armstrong et al., 2002), which suggests that minerals drive deep flux
130 by increasing aggregate density and by potentially protecting POC from degradation, since
131 both high and low latitude regions produce biominerals, predominantly opal and calcite
132 respectively (Francois et al., 2002). Recent studies, however, have only found evidence of
133 ballast acting to increase aggregate density, rather than performing any protective function
134 (Iversen and Robert, 2015).

135

136 In contrast, other work has focussed on water column temperature and dissolved oxygen
137 (DO) concentrations as key controls over interior processes since both play first-order roles in
138 respiration. A synthesis of all available estimates of the flux attenuation length scale (the
139 depth at which ~1/3 of the export flux remains) obtained from drifting neutrally buoyant
140 sediment traps demonstrated that cold environments have longer length scales (Marsay et al.,
141 2015; Figure 1a), consistent with the known role of temperature in regulating respiration and
142 viscosity (Taucher et al., 2014; Yvon-Durocher et al., 2012). This is, however, counter to the
143 patterns found by Francois et al. (2002) and Henson et al. (2012).

144

145 Devol and Hartnett (2001) originally proposed that DO may be an important control on
146 remineralisation. A synthesis of attenuation length scale estimated from export flux and deep
147 sediment traps (Henson et al., 2012) shows clearly that mesopelagic remineralisation is much
148 reduced at low DO concentrations (Figure 1b). Low DO concentration can cause oxic
149 respiration in sinking aggregates to become diffusion rather than substrate limited, with a
150 switch to nitrate respiration also possible (DO < 25 μM; Ploug, 2001; Ploug and Bergkvist,
151 2015). Additionally, modifications to DVM may occur as DO constrains DVM patterns
152 (Bianchi et al., 2013). Zooplankton may avoid low DO waters, reducing the depth to which
153 the active flux penetrates and/or the depth of particle fragmentation.

154

155 A final possibility is that the feeding ecology and metabolic pathways of organisms in the
156 interior play important roles. G14 infer that zooplankton permanently resident in the

157 mesopelagic (i.e. ones which do not undergo DVM) fragment, rather than ingest, the majority
158 of the particulate organic matter they encounter, converting much of it to smaller particles
159 which are then respired by prokaryotes with a minor fraction remaining as, or being
160 repackaged into, large particles such as faecal pellets. This fragmentation/repackaging
161 process likely reduces mean sinking velocity of POC and may be associated with enhanced
162 colonisation and degradation rates (Buesseler and Boyd, 2009). Mayor et al. (2014) further
163 speculate that zooplankton deliberately fragment detritus to stimulate the production of
164 nutritious and harvestable microbial biomass from poor quality organic material, termed the
165 'microbial gardening hypothesis'.

166

167 The lack of consensus about the relative importance of the processes involved in driving
168 mesopelagic respiration and particle flux attenuation has the practical consequence of
169 hindering the construction of an accurate representation of remineralisation for use in global
170 biogeochemical models. As a consequence, there is no consensus regarding how mesopelagic
171 remineralisation should be parameterised. No model can contain all possible processes and
172 the argument for including particular processes is often made in isolation (tempered by
173 computational efficiency) rather than from a perspective of how the processes interact. None
174 have a parameterisation grounded in an ecological and biogeochemical analysis of how the
175 mesopelagic zone functions.

176

177 In light of the requirement for realistic model representations of mesopelagic processes to
178 better quantify and constrain ocean carbon storage for the development of the UK Earth
179 System Model (ESM), and other ESMs contributing to IPCC assessments, the UK NERC
180 have funded a large integrated fieldwork and modelling programme aimed at understanding
181 and parameterising mesopelagic remineralisation processes: Controls over Ocean
182 Mesopelagic Interior Carbon Storage (COMICS). The importance of the biological carbon
183 pump in global climate regulation and our current inability to model it reliably has
184 implications for predictions of the carbon cycle; of the contemporary period, the past, and
185 predictions for future climate change. As such we believe that a high-level overview of the
186 work planned in COMICS will be of interest to a broad cross-section of the marine science
187 community, both nationally and internationally.

188

189 **Fieldwork**

190 The experimental approach of COMICS is to make observations of surface and mesopelagic
191 community structure and functioning in contrasting ocean locations where strong local
192 gradients in key parameters occur. A study site at South Georgia (SG) targets a region of
193 large gradients in ecosystem structure, whilst a study site in the Benguela upwelling system
194 has strong gradients in DO (Figure 1c, d).

195

196 South of SG productivity is relatively low with the community being dominated by small
197 phytoplankton taxa (Korb et al., 2012), and a high degree of surface recycling (Owens et al.,
198 1991). In contrast, north of SG, the Subantarctic Circumpolar Current Front interacts with the

shelf and slope introducing iron to the water column (Nielsdottir et al., 2014; Holeton et al., 2005) and causing an intense phytoplankton bloom characterised by large diatoms (Korb et al., 2012) and decreased surface recycling. Carbon export is higher in the northern region (Rembauville et al., 2015), with silica:carbon ratios in exported particles also different at the two sites (Le Moigne et al., 2014), potentially due to the well documented control iron plays in regulating silica:nitrogen ratios in diatoms (Takeda 1998; Hutchins and Bruland 1998). This frames the hypothesis that greater surface recycling and higher silica:carbon ratios will result in a deeper penetration of sinking particles into the interior at the southern site. Both sites are well oxygenated, and we therefore expect a strong active flux associated with DVM (Bianchi et al., 2013).

The second field study will focus on the role of DO by targeting the Benguela region where coastal upwelling supports intense production of organic matter, the sinking and respiration of which leads to the formation of a pronounced low oxygen zone (Shannon and Nelson, 1996; Mohrholz et al., 2008). Occupation of stations with differing DO will allow the hypothesis to be tested that the reduced oxygen layer, which is evident just below the thermocline, causes a deeper penetration of organic carbon due either to changes in DVM or to a reduction in aggregate respiration rates driven by low external DO and nitrate concentrations (Kalvelage et al. 2011; Fuessel et al. 2012).

Natural gradients within the study regions will not allow the role of temperature to be directly tested, although comparisons between the systems will be feasible, with the caveat that DVM patterns are likely to differ in the two systems. Two research cruises are planned for 2017/18 when gradients in primary production (for South Georgia), and DO (for Benguela) are maximal. On each cruise a full suite of measurements will be collected to characterise the carbon supply to the mesopelagic and the processes that control its attenuation (Table 1).

Synthesis and modelling

A hierarchical approach is required to achieve integration of the fieldwork into improved model forecasts. An initial data synthesis phase will bring together the estimates of organic matter supply and demand measured during the fieldwork and determine how these can be reconciled to produce a balanced carbon budget. This will highlight the processes that have the greatest influence on mesopelagic remineralisation and which should therefore be the focus of initial 1-D modelling efforts. Creation of a detailed process model (an extension of G14 to include improved depiction of zooplankton and microbial dynamics) will permit development of a range of models with sufficient realism to represent mesopelagic functioning accurately, yet which are sufficiently simple that they can be run in a global climate model. The challenge is to produce an interior food web model with the minimum complexity required to reproduce the budgets of interior flux and respiration.

Proper evaluation of the effect this foodweb model has on the global carbon cycle requires it to be run to equilibrium in a 3D framework to examine its predicted patterns of nutrient, carbon and oxygen distributions within the ocean interior. However, reaching equilibrium

242 requires a spin-up of many thousands of years and is too computationally expensive to
243 achieve using a full ESM. To sidestep this, the suitability of newly formulated alternative
244 parameterisations for future climate projections will be evaluated by determining their ability
245 to reproduce the global tracer field using the computationally efficient Transport Matrix
246 Modelling approach (Khatiwala, 2007; Bernardello et al., in prep). This effectively represents
247 ocean circulation and mixing via a computationally inexpensive matrix operation that allows
248 significantly accelerated model spin-up. A mechanistic, particle-based modelling approach
249 will also be pursued using the Transport Matrix Method, using the explicit simulation of a
250 large ensemble of marine particles and coagulation and disaggregation processes (Jokulsdottir
251 and Archer, 2016). Following this, the best parameterisation(s) will be implemented in
252 NEMO-MEDUSA (Yool et al., 2013), the coupled biophysical model selected for use within
253 UKESM1, the UK contribution to the next IPCC assessment.

254

255 While it is clearly important to determine whether the fieldwork and initial modelling efforts
256 result in different estimates of oceanic carbon storage, it is also important to understand how
257 – and why – this may change, both in the past and into the future, and what such changes
258 imply, both for our understanding of mesopelagic carbon cycling and, more broadly, the
259 global carbon cycle and climate feedbacks (Kwon et al. 2009; Roth et al. 2014). To address
260 this, forward simulations using the new parameterisation will allow us to study how the
261 functioning of the mesopelagic system may evolve as external forcing changes, and the
262 consequences of this for carbon storage.

263

264 **Perspective**

265 International policy and strategy on climate change mitigation and adaptation rely on the
266 most robust possible projections of future changes to CO_2 uptake and storage. A key part of
267 these projections lie in understanding the sustainability of, and reducing the impact on,
268 existing environmental services, e.g. atmospheric CO_2 modulation by the ocean. By
269 improving predictions of future ocean carbon storage, COMICS will contribute essential
270 knowledge for evidence-based policy-making in both of these areas.

271

272 COMICS has been carefully designed so that new insights into the mesopelagic carbon cycle
273 produced by leading-edge fieldwork will be directly translated into testable novel model
274 parameterisations, which will then be incorporated into the UK's community ESM. The
275 insights we gain will potentially have far-reaching influence, firstly via our innovative
276 fieldwork which will provide an unprecedented level of detail on mesopelagic carbon fluxes,
277 and secondly via our development of new parameterisations for carbon remineralisation.
278 These can be incorporated into any suitable global biogeochemical climate model, and have
279 the potential to influence future climate model development at the international level. The
280 need to better understand and model mesopelagic processes is underscored by increasing
281 international efforts, for example in the concurrent and complementary NASA programme
282 EXPORTS (Siegel et al., 2016), which will focus on field studies and modelling to support
283 and develop future satellite-derived estimates of upper ocean export fluxes and mesopelagic
284 remineralisation.

286 Mechanistic understanding of the processes that contribute to mesopelagic remineralisation
287 remains a major challenge for the oceanographic community, both for describing the present-
288 day carbon cycle and for projecting how this will interact with global climate change into the
289 future. The targeted fieldwork campaign and innovative modelling approach of COMICS will
290 enable significant progress towards filling this knowledge gap.

291

Author contributions

293 All authors are members of the COMICS project team and contributed to the programme's
294 development.

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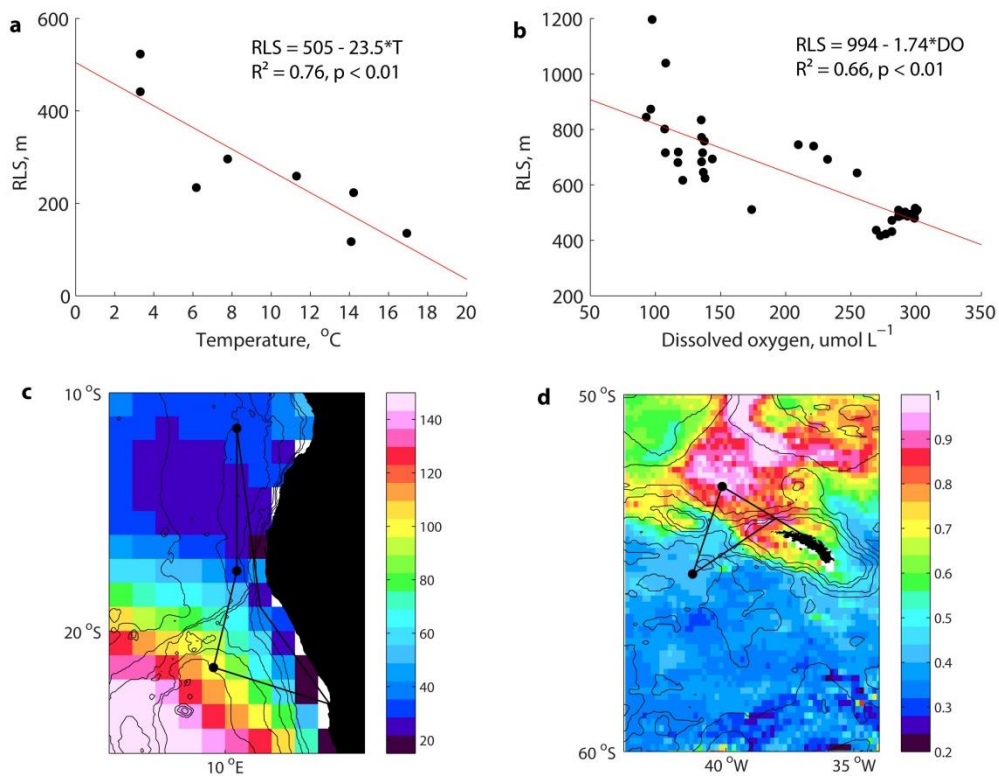
Figure 1: a) Remineralisation length scale (RLS) estimated from neutrally buoyant sediment traps deployed between 60 and 600 m depth plotted against 0-500 m mean temperature. Redrawn from a data compilation presented in Marsay et al. (2015). b) RLS estimated from thorium-derived export flux at 100 m depth and moored sediment traps at 2000 m depth (from data presented in Henson et al., 2012) plotted against 0-500 m mean dissolved oxygen concentration. For both a) and b), environmental data are from the World Ocean Atlas 2013 (Locarnini et al., 2013; Garcia et al., 2013). Results from Ordinary Least Squares regression are shown. c) Climatological minimum dissolved oxygen concentration (μmol L^{-1}) in July in Benguela upwelling region (Garcia et al., 2013). d) Climatological satellite-derived primary production (gC m^{-2}) in December in the South Georgia region (estimated from MODIS data using the algorithm of Behrenfeld and Falkowski, 1997). In c) and d) black dots and lines show potential cruise track and major process stations.

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456 **Table 1:** Observations planned for the COMICS fieldwork phase.

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Observation	Method
Flux attenuation and carbon supply to the mesopelagic	PELAGRA traps (6 total per deployment) with poisoned, unpoisoned, and gel collectors
	High speed camera (mounted on PELAGRA to estimate *in situ* particle sinking velocities, particle abundance and size distribution)
	In situ camera profiles for particle abundance and size distribution
	Marine Snow Catcher (to distinguish between fast and slow sinking particles)
	DOC supply (along and across isopycnals)
	Chemosynthesis
	Diel vertical migration and active export by zooplankton (MOCNESS and acoustics)
Pelagic biogeochemistry, upper-ocean food web	Nutrients, dissolved oxygen, DOC
	Size-fractionated biomass, chlorophyll and primary production
	Microbial community composition (molecular work)
	Particulate organic carbon, particulate organic nitrogen, particulate silica, particulate inorganic carbon
	Bulk and compound-specific stable isotope analyses
	Organic geochemical tracers (lipids, amino acids, pigments)
	Silica uptake and particulate inorganic carbon production
	Surface recycling (nitrate and ammonia uptake)
	Zooplankton feeding rates and turnover of C, N and fatty acids
	Fecal pellet production rates
Interior respiration	Zooplankton taxonomy and respiration (allometrically determined)
	Respiration on aggregates (ex-situ using microelectrodes; nitrate-based)
	Prokaryotic production (ex-situ; particle-attached and free-living)
	Bacterial growth efficiency (ex-situ; ^{14}C-leucine, ^{33}P-ATP, ^{35}S-Methionine uptake)

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