The Biological Carbon Pump in the North Atlantic

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ABSTRACT

Mediated principally by the sinking of organic rich particles from the upper ocean, the Biological Carbon Pump (BCP) is a significant component of the global carbon cycle. It transfers roughly 11 Gt C yr^{-1} into the ocean's interior and maintains atmospheric carbon dioxide at significantly lower levels than would be the case if it did not exist. More specifically, export by the BCP in the North Atlantic is ∼0.55–1.94 Gt C yr^{-1}. A rich set of observations suggests that a complex set of processes drives this export. However, significant uncertainties exist regarding the BCP in the North Atlantic, including both the magnitude of the downward flux and the ecological, chemical and physical processes by which it is sustained and controlled. Our lack of detailed mechanistic understanding has also hindered modelling attempts to quantify and predict changes to the BCP. In this paper, we assess current knowledge concerning the BCP in the North Atlantic in order to identify priorities for future research, as well as suggesting how they might be addressed.

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Introduction

Photosynthetic production of organic carbon by marine phytoplankton accounts for about half of the carbon fixation associated with global primary production (Field et al., 1998; Behrenfeld et al., 2006; Arrigo, 2007). A major component of both the oceanic and the global carbon cycles is the Biological Carbon Pump (BCP), which transfers this organic carbon, mostly as sinking particles, from the sunlit surface waters to the deep ocean (Sigman and Boyle, 2000; Boyd and Trull, 2007). Other contributions to this carbon transfer include the subduction of dissolved organic carbon (DOC) and the active transport of carbon by vertically migrating zooplankton (Hansell, 2002; Hansell et al., 2012; Steinberg et al., 2008).

Currently the ocean is thought to be the largest active carbon dioxide (CO_2) sink, dominating the terrestrial and atmospheric reservoirs, and absorbing more than a quarter of anthropogenically released CO_2 (Sabine et al., 2004). It has been estimated that present day atmospheric CO_2 concentrations would be approximately 200 ppm (∼50%) higher if the BCP did not exist (Parekh et al., 2006). The magnitude of global annual carbon export (11 Gt C) is more than three times larger than the annual accumulation of CO_2 in the atmosphere due to anthropogenic processes (3.2 Gt C) and five times larger than the annual net flux of CO_2 into the ocean (2.2 Gt C) (IPCC, 2007). Consequently, small changes in primary production and/or carbon export fluxes can significantly affect the magnitude of the BCP, and, through this, ocean–atmosphere CO_2 partitioning (Rost et al., 2008). These changes might occur due to climatically driven effects, such as increases in atmospheric and oceanic CO_2 concentrations, ocean stratification and circulation, dust deposition, and decreasing pH, may all affect the operation of the BCP. Understanding the BCP and its sensitivity to change is thus a research priority with far reaching implications. This paper examines the North Atlantic BCP primarily because of its significant role in global ocean circulation and biogeochemistry, but also because of its long history of measurement and its relevance to Western Europe and North America.

Like any ocean basin, the complex three dimensional circulation of the North Atlantic is critical in the redistribution of nutrients and subduction of organic material, and many features are common to

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other basins: the double gyre system of the subtropical and subpolar regions separated by a strong transition zone (the North Atlantic Current) (Sverdrup, 1947; Stommel, 1948; Munk, 1950), upwelling on the eastern margin (Schmitz and McCartney, 1993) and an active eddy field (Heywood et al., 1994; Oschlies and Garcon, 1998; Chelton et al., 2007). Additionally, the subpolar North Atlantic has areas of deep winter convection (Pickart et al., 2002), several regions (Nordic Seas) being globally important sites of deep water formation (Dickson et al., 2002). From a biogeochemical perspective, such regions are important in providing a shortcut from surface waters, in regular contact with the atmosphere, to deep waters that may be out of contact with the atmosphere for hundreds to thousands of years (Östlund and Stuiver, 1980). The subduction of unused macronutrients from these waters, possibly due to iron control over primary production, represents an inefficiency in the Biological Carbon Pump.

In the southern part of the North Atlantic, the central oligotrophic gyre occupies the majority of the subtropics and is largely aseasonal (Laws et al., 2000; Vantrepotte and Mélin, 2009). Further north, in the temperate and subpolar regions, enhanced nutrient supply to the surface ocean during winter convection, coupled with seasonal increases in light and temperature during the northern hemisphere spring, induce the onset of a phytoplankton bloom (Sieracki et al., 1993). The North Atlantic is characterised by a strong spring diatom bloom (Pommier et al., 2009), beginning in the shallow North Sea and adjacent open ocean areas in March (McQuatters-Gollop et al., 2007). This annual peak in diatom abundance propagates north through the subpolar North Atlantic during April and May (McQuatters-Gollop et al., 2007), generating a strong seasonal pulse of rapidly sinking carbon (Honjo and Manganini, 1993; Buesseler, 1998; Martin et al., 2011). Following the diatom dominated spring bloom, the North Atlantic experiences some of the most extensive coccolithophore blooms on the planet (Fernandez et al., 1993; Holligan et al., 1993; Brown and Yoder, 1994; Raitsos et al., 2006), with non-bloom coccolithophore communities persisting into late summer (Poulton et al., 2010).

These phytoplankton blooms are important not just in terms of primary production, but because of the associated production of sticky transparent exopolymer particles (TEP) and biominerals (opal and calcite), both of which have been implicated in accelerated transfer of organic material to depth (Armstrong et al., 2002; De La Rocha and Passow, 2007). In the summer, several regions of the subpolar North Atlantic (e.g., Iceland Basin) may exhibit high nutrient low chlorophyll (HNLC) conditions, with macronutrient concentrations often well above limiting levels despite shallow mixed layers (Sanders et al., 2005). This may be linked to widespread iron limitation within the resident phytoplankton community (Nielsdóttir et al., 2009).

Zooplankton play a critical role in the BCP, repackaging organic carbon produced via photosynthesis into faecal pellets and enhancing the speed at which it sinks out of the euphotic zone (Turner, 2002). At the same time, different zooplankton species consume sinking particles, respiring part of their content at different layers of the water column. Across the North Atlantic, during the spring bloom zooplankton biomass increases with latitude from $\sim$400 mg m^{-2} at 18°N to $\sim$3000 mg m^{-2} at 58°N (Lenz et al., 1993), and hence it may be hypothesised that the influence of zooplankton on vertical carbon flux also increases with latitude. Furthermore, the strong seasonal diatom bloom (Pommier et al., 2009) is the basis for secondary production of the dominant mesozooplankton *Calanus* spp. (Greene et al., 2003; Gislason, 2005). However, increasing temperatures have resulted in a northward shift in the biogeography of *Calanus* species: an increase in the abundance of *Calanus helgolandicus* and a decrease in the abundance of *Calanus finmarchicus* in the temperate North Atlantic (Bonnet et al., 2005); an increase in *C. finmarchicus* and a decrease

in *Calanus glacialis* in the Arctic Ocean (see Hirche and Kosobokova, 2007). As *Calanus* species have varying feeding preferences (Meyer-Harms et al., 1999; Irigoien et al., 2000), different life-history strategies (Madsen et al., 2008), different vertical distributions and seasonal peak abundances (Jónasdóttir et al., 2005; Jónasdóttir and Koski, 2010), it is reasonable to assume that shifts in *Calanus* biogeography, particularly when relative to concomitant changes in phytoplankton community structure and spring bloom timing, will have consequences for export (Wassmann, 1998). In addition to *Calanus* spp., the importance of small copepods ($\sim$1 mm) in the North Atlantic is increasingly recognised (Pitois and Fox, 2006). The small species typically dominate the biomass in late summer when *Calanus* spp. has entered diapause, a physiological state of dormancy (Madsen et al., 2008), and can in some areas be extremely abundant (Dugas and Koslow, 1984; Tang et al., 2011). Although many of the small species do not perform dial vertical migration, their grazing impact on the phytoplankton community can exceed that of *Calanus* spp. (Morales et al., 1991). Further, some of the most abundant small species are known to colonise aggregates, and can potentially consume a large part of the sinking particles before they leave the euphotic zone (Kiørboe, 2000; Koski et al., 2005).

The fraction of primary production that is ultimately exported is strongly dependent on the trophic mismatch in peak abundance between producers and consumers and on the capacity of the pelagic microbial community to remineralise particulate organic matter (Wassmann, 1998). In extreme cases as much as 70% of primary production has been observed to leave the euphotic zone through the sinking of individual cells and particles (Lignell et al., 1993). Typically, however, only 10–30% of material produced via primary production sinks below 100 m (Wassmann et al., 2003; Thomalla et al., 2008; Buesseler and Boyd, 2009). As this sinking organic material continues its downward journey through the oceanic twilight zone ($\sim$100–1000 m), up to a further 90% may be remineralised back into dissolved inorganic and organic forms by heterotrophic activity (Martin et al., 1987; Buesseler and Boyd, 2009). Only $\sim$1% of surface primary production is thought to be sequestered in the deep ocean (Ducklow et al., 2001; Poulton et al., 2006).

Given the above context, this paper is intended to serve two purposes. In Part 2, we briefly review current understanding of the BCP in the North Atlantic. Specifically we discuss, in the context of the North Atlantic:

– The strength of the BCP.
– The attenuation of carbon flux with depth.
– Modelling the BCP.

With this background, in Part 3 we then identify the priorities for future research, drawing upon the inherent complexities of the BCP as outlined in Part 2, but focussing on five key areas:

– Marine snow.
– Zooplankton.
– Geochemical constraints on the extent and stoichiometry of production.
– Empirical algorithms for flux attenuation.
– Modelling.

From the outset it is important to be clear on terminology. Throughout the paper we refer to the downward flux of material at the base of the euphotic zone (taken here to be the depth of 1% of incident irradiance) as 'export', which may be seen as the 'strength' (i.e. magnitude) of the BCP. We are unable to restrict this definition to a fixed absolute depth (for example 50 m or 100 m) due to the discrepancies in the methodologies employed to

measure export (see below). The choice of euphotic zone depth is far from a perfect solution (it is a relative measure that does not represent the absolute surface irradiance) but is considered the lesser of the various evils. Carbon fluxes measured at or below ~1000 m are referred to as 'sequestration fluxes', based on the assumption that sequestration lasting decades or longer only occurs when organic carbon sinks below the maximum depth of the winter mixed layer, and thus is unable to be immediately mixed back up to the surface ocean where exchange with the atmosphere is possible (Buesseler et al., 2007b). The ratio of export flux to total primary production we refer to as the e-ratio, and the ratio of sequestration flux to export flux as transfer efficiency (T_{eff}) (Honjo et al., 2008; Buesseler and Boyd, 2009). The term 'particle' is used to describe both single algal cells and constituent parts of marine snow aggregates. The term aggregate is restricted to describe collections of individual particles held together by an organic matrix, such as TEP.

Current understanding of the north Atlantic Biological Carbon Pump

The strength of the Biological Carbon Pump in the North Atlantic

Estimates of the magnitude of the BCP in the North Atlantic (0–80°N) suggest an annual export of between 0.55 and 1.94 Gt C yr^{-1}, with an average of 1.27 Gt C yr^{-1} (Table 1). Despite the use of different methodologies (discussed in Sections 'Geochemical budgets, ^{15}N uptake, Radioisotope deficits, Particle size spectra, Sediment traps, Satellite remote sensing and Comparison of estimates for the North Atlantic') and variability in how the flux is estimated (e.g. nutrient removal, quantification of sinking particles, organic matter formation and remineralisation; Sections 'Particle formation, Particle sinking and Particle degradation/remineralisation'), these estimates are surprisingly consistent, indicating a broad consensus.

Geochemical budgets

Over appropriate time and space scales, and under the assumption of steady state conditions, the upward supply of nutrients, new to the euphotic zone on an annual timescale (often referred to as new production), should balance the downward export of organic material (Eppley and Peterson, 1979; Christian et al., 1997). However, there is uncertainty about the magnitude of both new and total primary production within the subtropical ocean (Hayward, 1991; Painter et al., 2007) arising from new production estimates, from oxygen based methods and from quantifying the upward flux of ^{3}He, that exceed directly measured rates of (net) primary production (e.g. Jenkins, 1982; Jenkins and Goldman, 1985). The new production estimates obtained by Jenkins (1982) and Jenkins and Goldman (1985) of between 50 and 55 g C m^{-2}-yr^{-1} for the subtropical regions of the North Atlantic are high compared to observations of primary production based on in situ observations localised in time and space, potentially due to the latter missing ephemeral events associated with mesoscale and submesoscale processes. We have scaled up the estimates of new production from the above geochemical studies to give values for the entire subtropical North Atlantic (Table 1), yielding an export flux of 1.23–1.32 Gt C yr^{-1}. This approach cannot reliably be scaled to cover the entire North Atlantic due to important ecological differences between the subtropical and subpolar regions. As these geochemical estimates of new production are broadly similar to other export fluxes for the entire North Atlantic (Table 1), this is clearly one of several areas in which work is needed to better constrain measurements and understand how differences in methodology can lead to significantly different estimates of export.

^{15}N uptake

The measurement of nutrient uptake rates with the stable isotope ^{15}N have traditionally been used to provide an estimate of new (export) production through the f-ratio concept (the f-ratio being the fraction of primary production supported by allochthonous nutrients, and, by extension, the fraction of primary production that is new production) (Dugdale and Goering, 1967; Eppley and Peterson, 1979). Eppley and Peterson (1979) derived a simple relationship between total production and new production based upon a small dataset of direct observations, which was then applied to a globally extensive set of primary production measurements to estimate global new/export production. As this remains a key baseline study we include their observations in Table 1, but have scaled their results for the entire Atlantic Ocean to the smaller North Atlantic region, by using the ratio of the respective areas, to give an estimated annual new production rate of 1.13 Gt C yr^{-1}. More recently, however, the ability of the f-ratio based on nitrate uptake to estimate new production has been questioned on methodological and theoretical grounds. Particular criticism has focused upon measurements in oligotrophic waters where nitrification within the euphotic zone may play a significantly more important role than previously realised and where f-ratios may be substantially biased by the inclusion/omission of additional nutrients (e.g. urea) (Wafar et al., 1995; Lipschultz, 2001, 2008; Zehr and Ward, 2002; Martin and Pondaven, 2006; Painter et al., 2007; Yool et al., 2007).

Radioisotope deficits

Downward sinking particles scavenge the ^{234}Thorium (^{234}Th) radiochemical tracer from the upper ocean, by adsorption onto their surface. This leads to a measurable deficit of ^{234}Th in surface waters relative to the parent isotope ^{238}Uranium (^{238}U), which when utilised in conjunction with the POC: radionuclide ratio provides an estimate of carbon export flux (Buesseler et al., 1993; Sarin et al., 1999; Stewart et al., 2005; van der Loeff et al., 2006; Thomalla et al., 2008; Verdeny et al., 2008). ^{234}Th is utilised to estimate short term (monthly) fluxes due to its similar half life (~28 days) and is an increasingly common technique (Verdeny et al., 2009). We have estimated a North Atlantic ^{234}Th export flux based upon the compilation of observations reported by Henson et al. (2011). These authors show a strong correlation between the export ratio, the fraction of primary production exported estimated by comparing ^{234}Th derived POC export and primary productivity estimates from satellites, and sea surface temperature. However, these observations are spread widely across the North Atlantic and were obtained at different times of year. To obtain an annual estimate for the whole North Atlantic we used the following approach. First, as each observation represents a mean estimate over just 3 weeks we converted this to an annual estimate by dividing through by the fraction of annual export that takes place in the month in which the sample was taken. Lacking data for the seasonal cycle of export we used the MEDUSA model (Yool et al., 2011) to calculate the climatological monthly export in 10° latitudinal bands using output for the years 1996–2005. The fraction of export taking place in each month for each band was simply calculated by dividing each month's export value by the total annual export for that band. Second, we grouped the now annual estimates for export into 10° latitudinal bands, from the equator to 80°N. The estimates within each band were averaged to give an annual export as gC m^{-2} y^{-1} for each band. Finally, the estimate for each band was multiplied by the area occupied by each band, and the result from each band summed up to give a total estimate for the export flux integrated over the whole North Atlantic between the equator and 80°N of 2.2 Gt C yr^{-1}.

Table 1
A cross section of methodologies that can be used to provide estimates of export flux. For consistency, and where possible, export flux estimates have been scaled to identical areal extents and represent fluxes within the North Atlantic (0–80°N) unless otherwise stated.

Technique	Source data and units	Global export flux (Gt C yr^{-1})	N. Atlantic export flux (Gt C yr^{-1})	% of global export	Region	Reference and notes
[15]N uptake (f-ratio)	2.18 Gt C yr^{-1} for the entire Atlantic Ocean	4.7	1.13[a]	24	N. Atlantic (0–80°N)	Eppley and Peterson (1979) Relative to depth of euphotic zone
Geochemical budgets ([3]He and Oxygen utilisation)	55 g C m^{-2} d^{-1}	–	1.32[b]	–	Subtropical N. Atlantic (15–45°N)	Jenkins (1982)
Geochemical budgets (Seasonal oxygen cycle)	50 g C m^{-2} d^{-1}	–	1.23[b]	–	Subtropical N. Atlantic (15–45°N)	Jenkins and Goldman (1985)
CZCS chl-a-nitrate relationship (new production)	0.8 Gt C yr^{-1} for area of 3.41×10^{13} m^2	–	1.0[a]	–	North Atlantic (0–80°N)	Campbell and Aarup (1992)
Satellite SST, chl-a and f-ratio derived relationship	–	12.9[c]	1.42[c]	11	North Atlantic (0–80°N)	Laws et al. (2000)
Satellite SST, chl-a and pe-ratio derived relationship	–	18.9[d]	1.7[d]	11	North Atlantic (0–80°N)	Dunne et al. (2007)
		9.59[e]	1.94[e]	20	North Atlantic (0–80°N)	Henson et al. (2011)
Satellite SST, chl-a and [234]Th derived relationship	–	5[d]	0.54[d]	11	North Atlantic (0–80°N)	
[234]Th	Multiple sources	–	2.68[f] 2.2[g] (0.88) 2.45[h]	–	North Atlantic (0–80°N)	Based on: Charette et al. (1999), Santschi et al. (1999), Charette et al. (2001), Moran et al. (2002), Moran et al. (2003) Thomalla et al. (2006) and Le Moigne (unpub.)
Foodweb model	–	9.6[c]	1.44[c]	13	North Atlantic (0–80°N)	Laws et al. (2000)
Sediment Traps	2.47 Gt C yr^{-1} for the entire Atlantic Ocean (65°S–65°N)	–	1.29[a]	–	N. Atlantic (0–80°N)	Antia et al. (2001) Relative to winter mixed layer depth
Mean			1.27[i]	15		

[a] Recalculated from original source material using North Atlantic (0–80°N) areal estimate of 4.345×10^{13} m^2.
[b] Recalculated from original source using a subtropical (15–45°N) areal estimate of 2.46×10^{13} m^2.
[c] Estimates based on AVHRR SST data and VGPM production model.
[d] Estimates calculated using the relevant source algorithms, AVHRR SST data and Carr (2002) primary production model.
[e] Estimate derived from Table 2 of Dunne et al., 2007. Reason for discrepancy due to use of NCEP reanalysis data in original study.
[f] Estimate based on simple mean of all [234]Th observations.
[g] Estimate calculated as described in Section 'Radioisotope deficits'. Value in parentheses is NEMO/MEDUSA export flux estimate (Yool et al., 2011).
[h] Thorium based export at 100 m using median (as data distribution is non-normal) thorium measurement and N. Atlantic area of 5×10^{13} m^2.
[i] Mean calculated without estimates of Jenkins (1982) and Jenkins and Goldman (1985) and without [234]Th estimates.

Particle size spectra

Traditionally, it has been thought that sinking speeds of typical marine particles follow simple Stokes' law relationships, increasing with particle size but also being influenced by their excess density (relative to seawater) and porosity of the particle (Johnson et al., 1996). However, studies of marine snow aggregate sinking speeds indicate that Stokes' law does not accurately estimate particle sinking speeds due to the fractal geometry of most aggregates (which results in a different distribution of pore space for the same porosity than in a non-fractal particle) (Vicsek, 1989; Logan and Wilkinson, 1990; Jackson and Burd, 1998). Marine snow aggregates appear to sink several times slower than spheres of the same mass and density (Alldredge and Gotschalk, 1989). In order to better understand particle sinking speeds data bases of particle size, morphology and sinking speeds are needed (McDonnell and Buesseler, 2010). A range of in situ digital imaging techniques are now available to quantify particle size distributions throughout the water column (Stemmann et al., 2004) and studies are being undertaken to quantify size-specific carbon fluxes (Guidi et al., 2008). However, such work is ongoing and no estimates of North Atlantic export or sequestration fluxes using this technique are yet available.

Sediment traps

There is a rich and diverse literature on export flux measured by sediment traps, which allow simultaneous geochemical and microscopic analysis of the nature of the flux and the rate of flux attenuation with depth (Martin et al., 1987).

Comparisons between tethered sediment trap and radionuclide based export estimates in the top 1000 m indicate a mismatch in flux estimates due to under-trapping effects in the sediment traps (Scholten et al., 2001). This led to the development of drifting neutrally buoyant traps with improved trapping efficiencies (Buesseler et al., 2007a; Lampitt et al., 2008). Neutrally buoyant sediment traps have so far been primarily used in focussed process studies of flux attenuation in the top 1000 m, over short-term and local scales (e.g., Salter et al., 2007; Martin et al., 2011), and these technologically complex devices have not yet been used frequently enough to allow global or even regional estimates of export over the annual cycle, typically being deployed for just a few weeks.

Deep (>1000 m) tethered sediment traps, however, are particularly useful for estimating the sequestration flux into the deep ocean (Honjo and Manganini, 1993; Antia et al., 2001) and provide the only measurements of seasonal and inter-annual variability in fluxes. Converting these deep estimates of sequestration flux to estimates of export flux at shallower depths requires the extrapolation of the deep flux, often over several vertical kilometres across which the flux may increase by an order of magnitude. Often this extrapolation is carried out using the Martin curve (Martin et al., 1987; Lutz et al., 2007). (For a more detailed discussion of the Martin curve and flux attenuation see Section 'Attenuation of carbon flux in the North Atlantic') However, recent studies have indicated

that, at the very least, the parameters associated with the curve are not spatially uniform, so that a single parameterisation may not be applicable across the whole North Atlantic, let alone the global ocean (Buesseler et al., 2007b).

A synthesis of sediment trap data prepared by Antia et al. (2001) estimated a North Atlantic sequestration flux to waters beneath the winter mixed layer depth of 1.29 Gt C yr^{-1}. This implies a transfer efficiency of order 50% which is larger than that calculated by Henson et al. (2012) and should be viewed as an upper limit. An alternative global estimate of 0.43 Gt C yr^{-1} at 2 km based on deep sediment traps and particle attenuation with depth is also available (e.g. Honjo et al. (2008)).

Satellite remote sensing

Both seasonal and spatial variability in the strength of the BCP make it difficult to extrapolate from point observations or measurements to annual, regional or basin scale estimates. Realistically, satellites are the only way we can currently obtain synoptic, basin wide measurements of the BCP. However, satellite based methods for estimating export fluxes are only as good as the understanding of marine ecosystems and biogeochemistry which underpin them.

An early attempt to estimate new production in the North Atlantic was presented by Campbell and Aarup (1992), who estimated the magnitude of annual new production based upon the seasonal removal of nitrate and surface chlorophyll data measured with the Coastal Zone Colour Scanner (CZCS). They developed an approximate relationship based upon observational data that related winter nitrate concentrations, the seasonal formation/deepening of the nitracline (the depth below which nitrate concentration is >1 μmol N kg^{-1}), and the onset of oligotrophy to estimate a new production rate of 1 Gt C yr^{-1} for the North Atlantic.

Since this initial attempt, several more advanced algorithms to estimate export flux have been developed. All utilise satellite data (*e.g.* surface chlorophyll fields, sea surface temperature), a model of primary production (estimated from surface chlorophyll) and relationships derived from global observational datasets. *Laws et al. (2000)* derived an *f*-ratio based algorithm which we have used to produce a North Atlantic export estimate of 1.42 Gt C yr^{-1}. In recalculating this estimate we have used the Vertically Generalised Production Model (VGPM) (Behrenfeld and Falkowski, 1997), AVHRR SST, and SeaWiFS surface chlorophyll fields. Thus our estimates are slightly different to those reported by Laws et al. (2000).

Using a method (*pe*-ratio) similar to that of the *f*-ratio approach, Dunne et al. (2007) give a second estimate for the North Atlantic export flux of 1.7 Gt C yr^{-1}. Note that the export estimate we present here is smaller than that reported in Table 2 of Dunne et al.

(2007) due to differences in the input fields we use (specifically SST). A recent alternative to the *f*-ratio and *pe*-ratio approaches was presented by Henson et al. (2011) who utilised a global database of ^{234}Th export flux measurements to derive a globally applicable export algorithm. This approach produces a North Atlantic export estimate of 0.54 Gt C yr^{-1}, roughly a third the size of the other two estimates (note that the estimates in Table 1 from Dunne et al. (2007) and Henson et al. (2011) include a DOC contribution, roughly 20% of total export). The disparity highlights the degree to which we still do not understand the first order processes involved in the BCP.

Remote sensing algorithms for estimating primary production and export are particularly sensitive to SST, and the magnitude of both global and regional export estimates are further dependent upon the underlying primary production model. As several different production models and SST products exist we demonstrate the variability in performance between three export algorithms (Laws et al., 2000; Dunne et al., 2007; Henson et al., 2011) to highlight the difficulties in estimating export in this way (Table 2). For consistency we utilise the Carr (2002) primary production model and use SeaWiFS surface chlorophyll and AVHRR or WOA SST products. This analysis reveals that changing the SST product can have significant impacts upon the magnitude of global export produced by all three algorithms. Using the Laws et al. (2000) algorithm we estimate an export flux of 1.52–1.61 Gt C yr^{-1} for the North Atlantic, which represents 11–15% of global export production. The reason for the difference between these estimates and the estimate provided in Table 1 is due to a change from the VGPM to Carr (2002) production models. Using the Dunne et al. (2007) algorithm we estimate similar export fluxes for the North Atlantic of 1.47–1.7 Gt C yr^{-1} which represents 9–17% of global export. Despite changes in the global export production, due to changes in the underlying SST fields, export estimates from these two algorithms provide comparable estimates for the North Atlantic. The third algorithm is from Henson et al. (2011). This produces lower overall export fluxes of 0.5–0.54 Gt C yr^{-1} for the North Atlantic but a similar global proportion (11–15%) compared to the other two algorithms. Thus whilst there is some uncertainty over the magnitude of global export between these three algorithms, and indeed over the magnitude of export within the North Atlantic, all are broadly consistent in their estimates of the proportion of global export occurring within the North Atlantic.

Comparison of estimates for the North Atlantic

The various methodologies summarised in Table 1 provide an average North Atlantic basin wide export estimate of 1.3 Gt C yr^{-1}, with a range in estimates from 0.5 to 2.7 Gt C yr^{-1}. The majority of

Table 2

Demonstration of the sensitivity of export flux algorithms to the SST product used. Note that despite large changes in the overall magnitude of the global export flux when using either World Ocean Atlas (WOA) or Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature, export fluxes in the North Atlantic are both relatively constant in magnitude and also in their proportion of global export which indicates areas outside of the North Atlantic are more responsive to differences in SST. For comparative purposes all estimates are based on the Carr (2002) primary production model and consistent chlorophyll and SST fields. Export estimates from Henson et al. (2011), and Dunne et al. (2007), have been scaled to include an additional (25%) export flux due to DOC, a requirement not considered necessary for the export estimates from Laws et al. (2000)., which are considered to include the DOC mediated flux already.

Technique	SST product	Global export flux (Gt C yr^{-1})	N. Atlantic (0–80°N) export flux (Gt C yr^{-1})	% of global export	Reference
Satellite chl-a, SST and f-ratio derived relationship	WOA SST	10	1.52	15	Laws et al. (2000)
	AVHRR SST	14.7	1.61	11	
Satellite chl-a, SST and pe-ratio derived relationship	WOA SST	8.6	1.47	17	Dunne et al. (2007)
	AVHRR SST	18.9	1.7	9	
Satellite chl-a, SST and ^{234}Th derived relationship	WOA SST	3.39	0.5	15	Henson et al. (2011)
	AVHRR SST	5	0.54	11	

individual estimates are broadly similar though there are a few exceptions and, curiously, one particular technique is associated with both the highest and lowest export estimates. Based upon limited in situ observations with the [234]Th technique we have calculated an export flux of 1.9–2.7 Gt C yr^{-1}. Using the same data but in conjunction with satellite and primary production algorithms Henson et al. (2011) estimate an export flux of only 0.5 Gt C yr^{-1}. That different methods of extrapolating the same measurements to annual timescales and basin length scales can have such a large discrepancy highlights the need for caution when comparing any estimates of export or sequestration.

The remaining studies provide export estimates that range from 1 to 1.9 Gt C yr^{-1} so it is appropriate to briefly consider methodological issues associated with these also. A large number of studies report estimates of nitrate based new production, which under the steady state assumption is equal to the export of material from the surface ocean. However few studies estimate new and export production independently and over seasonal timescales, so the validity of this assumption is largely untested. Indeed, where such comparisons have been done a significant decoupling between new production and export flux has been noted (Plattner et al., 2005; Morris and Sanders, 2011). In these two examples, export production was found to be greatly reduced relative to new production. Similar uncertainties undoubtedly underlie the first-order approximations we report here. However, oxygen based estimates of new production for the subtropical regions are as large as many estimates of export production over the entire North Atlantic basin. If one were to scale accordingly to the same areal extent, new production (based on oxygen) would be as high as 2.3 Gt C yr^{-1}, similar to the higher [234]Th estimates.

In summary, differences in methodologies and differences in what each technique measures, coupled with sparse observations remain major weaknesses in ongoing attempts to measure the strength of the BCP accurately in the North Atlantic.

Attenuation of carbon flux in the North Atlantic

Organic material sinking through the mesopelagic zone experiences significant heterotrophic consumption, resulting in a decrease in flux with depth (Buesseler et al., 2007b). The rate at which this decrease occurs with depth is often parameterised via the simple numerical formulation of (Martin et al., 1987). This empirically-derived model links the flux at depth z, $F(z)$, to the flux at the base of the euphotic zone (z_0), $F(z_0)$, via $F(z) = F(z_0) \cdot (z_0/z)^b$. The exponent, b, has become known as the Martin parameter with the function itself now commonly referred to as the 'Martin curve'.

This 'Martin Curve' has been widely utilised to calculate particle degradation in the ocean interior from export data (e.g. Najjar et al., 1992; Yamanaka and Tajika, 1996; Ito and Follows, 2005). It was initially derived by fitting the function to a set of downward particle flux measurements in the Pacific made using tethered sediment traps to give an estimate of b of 0.858 (Martin et al., 1987). The VERTIGO programme (Section 'Sediment traps') has revealed spatial variability in b, ranging from 0.51 to 1.33 in the Pacific (Buesseler and Boyd, 2009), with estimated values of b ranging from 0.43 to 1.7 in the Atlantic (Lampitt et al., 2008; Martin et al., 2011). In a recent satellite data based study, Henson et al. (2012) estimate spatially explicit values of b ranging from ∼0.3 to 1.1 globally and from 0.5 to 0.9 in the North Atlantic. There is also likely to be seasonal variability. Taking b values of 0.4 and 1.4 in turn corresponds to a significant difference (∼150 ppm versus ∼300 ppm of CO_2, respectively), in air–sea CO_2 partitioning (Kwon et al., 2009). However, the majority of current estimates of b are either based on globally modelled data sets or restricted to Pacific observations highlighting the need for further equivalent data from the North Atlantic, particularly in oxygen depleted regions where transfer efficiency is likely to be high (Devol and Hartnett, 2001).

Moreover, long term sediment trap studies (Steinberg et al., 2001; Lampitt et al., 2010) which highlight flux variability in the deep ocean, coupled to alternative flux parameterisations (Armstrong et al., 2002; Francois et al., 2002; Howard et al., 2006) raise the question of whether the Martin curve is too simplistic to capture the observed variability. Clearly the rate at which sinking material is degraded is unlikely to be spatially or temporally uniform, as required to be fully described by a single constant parameter such as b. Other factors such as particle formation mechanisms (Section 'Particle formation'), particle sinking speeds (Section 'Particle sinking') and degradation rates (Section 'Particle degradation/remineralisation') all play critical roles in the attenuation of particle flux in the ocean's interior and will now be briefly discussed.

Particle formation

Aggregation and plankton related processes all alter particle properties, for example by changing particle size, morphology and density, thereby influencing particle sinking speeds and export flux. Individual phytoplankton cells are generally too small to sink rapidly, regardless of their density, due to the viscosity of seawater (Smayda, 1970). Sinking velocities may be orders of magnitude greater when individual cells are incorporated into particles greater than 0.5 mm (Turner, 2002). Collectively, these large, sinking particles are known as marine snow. Although marine snow may incorporate the faecal pellets and moults of zooplankton, many consist of aggregations of phytoplankton cells, biominerals such as opal and calcite and lithogenic materials such as clays and dust, detritus and other Particulate Organic Matter (POM) (Alldredge et al., 1993; Simon et al., 2002; Turner, 2002; Burd and Jackson, 2009). These aggregates are held together by a "sticky" matrix such as TEP (Alldredge et al., 1993; Passow, 2002) or mucous-based feeding structures discarded by pteropods or appendicularians (Robison et al., 2005).

Aggregation of small suspended particles with dissolved and colloidal material produces larger particles, a process often thought to be driven by both physical processes such as Brownian motion, differential settling speeds and biological processes such as the production of TEP and zooplankton feeding (Jackson, 1990, 1995; Jackson and Burd, 1998; Burd and Jackson, 2009).

Diatoms are an important, although not exclusive, source of TEP in the surface ocean and may help to drive the aggregation of blooms in the ocean (Passow and Alldredge, 1995; Passow, 2000; Grossart et al., 2006; Gardes et al., 2011; Martin et al., 2011). Furthermore, TEP concentrations have been shown to have a greater influence on the formation of rapidly sinking aggregates than the concentration of phytoplankton cells (Logan et al., 1995). It has been suggested that without TEP, a phytoplankton bloom might never sink (Kiørboe et al., 1996). However episodic flux events from the North Atlantic spring diatom bloom associated with ungrazed, TEP-rich diatom aggregates have been observed, challenging this view (Martin et al., 2011).

Many of the deep N Atlantic sediments consist of rich calcareous oozes made up of coccolithophores, such as *Emiliana huxleyi*, *Gephyrocapsa muellerae*, *Calcidiscus leptoporus* and *Coccolithus pelagicus* (Ziveri et al., 2000), implying a significant role for these organisms in efficient export. Laboratory studies confirm that calcifying cells such as coccolithophores can enhance particle density and sinking speed (Engel et al., 2009). Seasonal and geographical changes in phytoplankton community structure can therefore exert significant control on the region's BCP.

This conclusion also extends to zooplankton community structure. These multicellular secondary producers create dense faecal pellets, appendicularian houses and mucus feeding nets, all of

which also enhance particle aggregation and sinking (Turner, 2002; Berline et al., 2011). In a simple sense, faecal pellets represent the re-packaging of small, slowly or non-sinking particles into larger, compact, fast sinking pellets which can be relatively rich in biominerals, depending on which phytoplankton the zooplankton grazed upon (Ploug et al., 2008). One study of faecal pellet export in the north east Atlantic estimated a flux of 7.5 mg C m^{-2} d^{-1} from the surface ocean (Dam et al., 1993); compared to, for instance, values of 0.1–1.5 mg C m^{-2} d^{-1} or up to 100 mg C m^{-2} d^{-1} which have been reported for different areas of the Arctic Ocean (Olli et al., 2007; Caron et al., 2004). One class of zooplankton, the appendicularians, produce and abandon up to 8 feeding houses per individual per day (Sato et al., 2001), forming a substantial proportion of sinking particles (Vinogradov, 2005) and contributing up to 40% of POC flux (Bauerfeind et al., 1997). Appendicularian abundance in the North Atlantic increased during the late 1980s (Kane, 2011), likely causing substantial interannual variability in particle flux.

Particle sinking

The measurement of sinking speeds for individual aggregates and faecal pellets is methodologically challenging, although they have been measured in both laboratory settling columns and in situ (Silver and Alldredge, 1981; Alldredge and Gotschalk, 1988; Hansen et al., 1996; Diercks and Asper, 1997; Engel and Schartau, 1999; Engel et al., 2009; Ploug et al., 2010). Integrated particle sinking speeds have also been estimated using sediment trap data (Xue and Armstrong, 2009). The resulting estimates of sinking speeds range over three orders of magnitude, between ~5 and 2500 m day^{-1}. However, the majority of aggregates and faecal pellets sink between a few tens and a few hundreds of metres per day (Turner, 2002). In the North Atlantic, sinking speed estimates from sediment trap bulk flux measurements range between 61 and 741 m day^{-1} (Fischer and Karajas, 2009; Xue and Armstrong, 2009).

The speed at which a particle sinks influences the vertical distance over which it is remineralised and thus the depth to which it transports biogenic carbon. For particles to sink they need to be both sufficiently large, to escape the constraints on sinking imposed by the viscosity of seawater, and denser than the surrounding fluid (De La Rocha and Passow, 2007). The density of POC and its geochemical constituents (e.g. amino acids and proteins) are very close to seawater (Francois et al., 2002). Compilations of deep sediment trap observations (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002) have led to the suggestion that the incorporation of biominerals (opal, calcite) and lithogenic material into sinking aggregates of POC can increase density and lead to enhanced particle sinking speeds – the so called ballast effect. More recently, evidence of biomineral ballasting in the euphotic zone of the North Atlantic has also been found (Thomalla et al., 2008; Sanders et al., 2010). However, the precise nature of the relationship between fluxes of POC and biominerals, such as how the two become associated in aggregates, remains unclear (De La Rocha and Passow, 2007).

A more nuanced approach, recognising that both size and density are important factors is now emerging (McDonnell and Buesseler, 2010). For example, the simplified classification of sinking speeds into fast, slow and suspended, used for some time by modellers (Fasham et al., 1990; Kriest and Evans, 1999; Boyd and Stevens, 2002), is now finding favour in observational studies. Alonso-González et al., 2010 suggest that, globally, slow sinking particles (0.7–11 m day^{-1}) constitute ~60% of the export flux, whilst fast sinking particles (>326 m day^{-1}) constitute ~25% of the export flux. More recently, data collected by *Riley et al. (2012)* suggest that in the northeast Atlantic, slow sinking particles contribute ~60% of the total export flux, appear largely unassociated with ballast material and are likely to be fully remineralised

in the upper twilight zone. In contrast, fast sinking particles are partially ballasted, contribute 40% of the total export flux and are likely to be more important for sequestration fluxes (Riley et al., 2012).

In addition to the production of faecal pellets (Section 'Primary production and export flux'), zooplankton also facilitate the sinking of POC via diel vertical migration (DVM) between the surface ocean and the mesopelagic zone (Steinberg et al., 2000). It is thought that DVM allows zooplankton to avoid predation by higher trophic level organisms (Loose and Dawidowicz, 1994). The production and defecation of POC at depth, transporting carbon through the water column, is known as the active transport flux (Steinberg et al., 2000). Simple estimates of the importance of the active flux measured in the North Atlantic suggest that it may significantly enhance the gravitationally mediated flux of material into the deep ocean by up to 53% (Yebra et al., 2005). An annual estimate of the active flux for the North Atlantic ranges from 0.5 to 1.5 g C m^{-2}-yr^{-1} (Morales, 1999) or 0.02–0.06 Gt C yr^{-1} for the North Atlantic as a whole, using the same area as for Table 1.

Particle degradation/remineralisation

Observational studies of the flux of organic material from the surface ocean through the mesopelagic to the deep ocean show a strong attenuation with depth. Remineralisation by bacteria and zooplankton of sinking POC is a major factor resulting in flux attenuation through the mesopelagic. Aggregates are hot spots for bacterial activity (Alldredge et al., 1986; Aristegui et al., 2009). Bacteria hydrolyse POC to dissolved organic carbon (DOC) and laboratory studies estimate POC specific respiration rates to be as high as 0.083 day^{-1} in aggregates (Ploug and Grossart, 2000). Zooplankton also graze on aggregates (Lampitt et al., 1993; Steinberg, 1995), and fragment larger aggregates into smaller ones (Goldthwait et al., 2004) which sink more slowly. Similar to bacteria, diverse zooplankton species can be many times more concentrated on or around marine aggregates relative to the surrounding water (Steinberg, 1995; Green and Dagg, 1997); in fact zooplankton consumption can potentially turn over the aggregate carbon within a few days (Kiørboe, 2000).

Comparison of bacterial remineralisation and zooplankton feeding rates from independent studies suggests zooplankton consumption results in a greater and more variable POC turnover than bacterial remineralisation, at least in the euphotic zone. Very little is known about the relative carbon demands of bacterial and zooplankton in relation to the attenuation of the POC flux. In the only study to date to construct a carbon budget of the twilight zone, Steinberg et al. (2008) found bacterial and zooplankton carbon demands between 150 and 1000 m to be similar but also individually higher than the total POC flux. They posit that zooplankton DVM and feeding in the surface waters must play an important role in satisfying the metabolic carbon demand (Karl et al., 1988; Steinberg et al., 2008). There is a clear need for similar investigations to be carried out in the North Atlantic (Burd et al., 2010).

Ecosystem structure is also an important determinant of particle attenuation. Particle attenuation at the picoplankton dominated Station ALOHA in the North Pacific subtropical gyre was much more pronounced than at the diatom dominated Station K2 (North Pacific subarctic gyre) (Buesseler et al., 2007b). Francois et al. (2002) suggest that ecosystem structure may regulate the efficiency of carbon transfer through the twilight zone. High latitude opal dominated regions may produce more labile material due to greater seasonality, a greater fraction of primary production being exported and less effective microbial loops, meaning greater remineralisation rates and lower transfer efficiency through the mesopelagic zone (Francois et al., 2002). Warmer, less seasonal, low latitude systems where calcite production

dominates biomineralisation (Poulton et al., 2006) may generate more refractory material as a result of more complex food webs and efficient microbial loops in the surface ocean, thus a higher fraction of the exported carbon flux may survive transit through the mesopelagic (Francois et al., 2002; Thomalla et al., 2008). Indeed, there is evidence (Henson et al., 2012) to suggest that at high latitudes e-ratio is high but transfer efficiency is low i.e. exported material is relatively labile, and vice versa at low latitudes. Similar conclusions have been reached by Lam et al. (2011) based on an analysis of an extensive global database of particulate profiles. They propose a paradigm of non-bloom environments with low transfer efficiencies with sporadic bloom environments, often diatom dominated, in which transfer efficiency is low. However, our understanding of the influence of ecosystem structure is limited, being based either on detailed observations that are restricted to the Pacific or on broader data set compilations at the global scale, indicating the need for studies focused on the North Atlantic.

Modelling the Biological Carbon Pump in the North Atlantic

Our present understanding of the BCP and the key drivers of downward export of biogenic particles is mostly based on global (e.g., Francois et al., 2002; Lutz et al., 2002; Dunne et al., 2005) and regional (e.g., Antia et al., 2001) syntheses such as NPP from satellite observations (e.g., Behrenfeld and Falkowski, 1997), comparisons among global models (Orr et al., 2001; Doney et al., 2004), and between models and biogeochemical observations (Laws et al., 2000; Moore et al., 2002a,b). The ability of models to quantify the downward flux of biogenic particles is central to determining the potential for climate change to impact the functioning of the BCP and the role of oceanic biogeochemical feedbacks in influencing climate in the future (Bopp et al., 2001; Feely et al., 2004).

Primary production and export flux

Several models have been developed with variable stoichiometry for a variety of processes including C/N uptake when extracellular excretion of DOC is included (e.g. Schartau et al., 2007). In additon processes such as ligand production and scavenging are beginning to be included in iron based models (Ye et al., 2009; Weber et al., 2007). In the Southern Ocean it appears that variability in iron concentrations can control the stoichiometric coupling between silicon and nitrogen, a process which can potentially control the functioning of the BCP in ocean regions remote from Antarctica which receive many of their nutrients from the Southern Ocean (Sarmiento et al., 2004).

Flux attenuation and sequestration

Oceanic carbon uptake is strongly influenced by the supply of nitrogen and phosphorous to photosynthetic marine plankton, and the stoichiometry, or elemental ratios, of carbon, nitrogen and phosphorus are therefore critical to the efficiency of the ocean carbon sink (Broecker and Henderson, 1998). The integrated effect of the different processes involved in export and remineralisation varies spatio-temporally, and this might be reflected in variability of sinking flux attenuation e.g. the Martin *b*-value (Martin et al., 1987; Kwon et al., 2009).

Some ecosystem models (e.g. Fasham et al., 1990; Blackford et al., 2004) include the breakdown of POM to DOM as a function of the nutritional content of the particulate fraction. Fluxes of the detrital nutrient component are derived from the carbon flux multiplied by the nutrient/carbon ratio of the particulate matter. Fluxes to the dissolved organic compartments are portioned between labile and semi-labile fractions according to a fixed parameter, whereas remineralisation of DOM is assumed to occur at a constant rate and sedimentation of detritus is governed by simple sinking rates.

Priorities for future research

Variability in the efficiency and overall activity of the BCP originates from variability in the formation, character, sinking velocity, and decomposition of the marine snow of large, rapidly sinking particles. Although this sounds relatively simple, as discussed above, numerous interacting factors and processes are involved in each of these aspects. During the last few decades, considerable progress has been made towards understanding the various contributing factors and processes (e.g. net primary production, aggregation, ballasting, and the activities of zooplankton and bacteria) (see reviews such as Alldredge and Silver, 1988; Jackson and Burd, 1998; Passow, 2002; Simon et al., 2002; Turner, 2002; Ziveri et al., 2000; Buesseler and Boyd, 2009; Burd and Jackson, 2009). This work needs to continue, and in addition, we need to better (inter-)connect our understanding of BCP processes (e.g. net primary production) with the observed regional and temporal variability of e-ratios and T_{eff} in the North Atlantic and other ocean basins. This will require consideration of how processes interact within different, dynamic ocean environments and food web structures.

Below we outline some priorities for future research on the BCP. Although we discuss each of these issues separately it should be emphasised that a key feature of any future research should be to follow a more integrated approach, considering the system as a whole rather than individual parts. Please note that the variety of new techniques emerging to study the BCP is tackled in more detail in a separate review (McDonnell et al., 2013).

Marine snow

Since the large, rapidly sinking particles known as marine snow constitute one of the major vectors of organic carbon transport out of the surface ocean, they remain a key priority for BCP research. There are two areas in particular where progress would move us closer to having a predictive understanding.

Laboratory studies of aggregate formation, degradation and remineralisation

Aggregates which form through the coagulation of phytoplankton and other forms of particulate organic matter constitute a significant fraction of the marine snow sinking through the ocean (Alldredge and Silver, 1988; Simon et al., 2002; Turner, 2002). In recent years, work in the laboratory using indoor rolling tanks, flocculators, and similar devices, has provided important information concerning the formation, character, composition, sinking velocity, and decomposition of marine aggregates (Ploug and Jørgensen, 1999; Kiørboe and Jackson, 2001; Simon et al., 2002; Goldthwait et al., 2004; Passow and De La Rocha, 2006; Passow et al., 2007; De La Rocha et al., 2008; Ploug et al., 2008; Engel et al., 2009; Gardes et al., 2011; Iversen and Ploug, 2010). Cylindrical rolling tanks (Shanks and Edmonson, 1989), for example, allow sinking particles to remain in suspension, enabling aggregates of POM (exopolymer-producing phytoplankton like diatoms and coccolithophores, faecal pellets, bacteria, microzooplankton, detritus), exopolymer particles, and ballast minerals (diatom frustules, detached coccoliths) to form following collisions between smaller sinking particles. These aggregates may then be immediately analysed for their properties and composition or used in experiments involving ballast minerals, zooplankton, or bacteria.

Although the theory behind the formation of aggregates has been reasonably well detailed (Burd and Jackson, 2009), biological

variability in the factors, such as the stickiness of TEP and other exopolymeric substances (EPS), necessary for aggregation needs considerable further empirical investigation. In addition, further work is needed to allow us to predict the sinking velocity of aggregates formed, a complicating factor being their fractal structure which undermines traditional measures of size (Alldredge and Gotschalk, 1989; De La Rocha and Passow, 2007).

The most urgent topic to be addressed in laboratory-based work with aggregates concerns the influences that interactions between phytoplankton and zooplankton or phytoplankton and bacteria have on aggregation, aggregates, and the decomposition and sinking of aggregates. This means investigating the influence of these interactions on TEP and EPS production, stickiness, and degradation, phytoplankton calcification and silicification, and, in general, on the formation, solubulisation, fragmentation, remineralisation, and sinking of aggregates.

For example, recent work has shown that the presence or high abundance of particular bacteria in the vicinity of certain diatom cells may trigger exudation of TEP (Gardes et al., 2011), driving aggregation at lower cell densities than usual. Other diatoms may not form TEP in the absence of specific bacteria (Gardes et al., 2011), making the aggregation of some diatom blooms dependent upon the abundance and activities of specific bacteria.

To give another example, it has been shown that grazing pressure could stimulate diatoms to increase their degree of silicification by as much as 100% (Pondaven et al., 2007). Such a large effect, which has not been studied with respect to its effect on particle sinking and flux, is likely to increase the potential ballast effect and therefore the sinking velocity of aggregates formed under such conditions. Conversely, the dissolution of calcite in zooplankton guts may reduce the availability of ballast minerals, diminishing the ballast effect. Modelling suggests that up to 15% of calcite associated with a coccolithophore bloom could dissolve during passage through zooplankton guts (Jansen and Wolf-Gladrow, 2001). As incorporation of calcite coccoliths into aggregates significantly increases their settling velocity (Engel et al., 2009) this could result in the increased residence time of POC in the euphotic zone and a greater fraction of NPP remineralising above the thermocline.

Following on this theme of interactions of different trophic levels, we also need to understand interactions between zooplankton and bacterial populations, and their impact on the formation, character, heterotrophic colonisation, and destruction of aggregates. For instance, predation by macrozooplankton on microzooplankton, who in turn may prey on bacteria, may alter bacterial population numbers and/or composition. Predation may also affect the colonisation of marine snow by both microzooplankton and bacteria, by allowing one group to increase at the expense of another. Differences in microzooplankton abundance will have an impact on the exudation of TEP and TEP-precursors (Gardes et al., 2011) and for that reason, an influence on aggregation rates (De La Rocha, unpublished). The balance between microzooplankton and bacterial populations living on aggregates is also likely to have an influence on the rate of degradation of the aggregates. Control of bacterial numbers by microzooplankton will additionally affect the microbial loop, the bacterial conversion of DOM to POM which provides a means by which non-sinking DOM can be converted into a form with potential for incorporation into aggregates. Likewise the release of bacterial ectohydrolases that help to solubulize POM and decompose DOM (and the exact ectohydrolases released) will be affected by the extent to which microzooplankton are impacting bacterial populations. Significant effort has been put into understanding the processes responsible for degrading faecal pellets which, under some circumstances, can form a significant fraction of POC flux. Zooplankton themselves were found to play a minor role in respiring faecal pellets with most ingested pellets being mechanically degraded and rejected once captured. Instead, protozooplankton and bacteria were found to be the dominant functional groups involved in degrading these particles (Poulsen and Iversen, 2008, Iversen and Poulsen, 2007). This tandem processing by zooplankton and bacteria in the respiration of organic matter has also been observed in the field (Iversen et al., 2010).

Mesocosm experiments

An effective strategy for exploring the ecological complexity of the BCP and its impact on the partitioning of NPP into sinking particles (versus its retention in the upper ocean food web) is to run nearshore or open ocean mesocosm experiments. This is a strategy that has, for instance, worked well for studies looking at the response of phytoplankton and surface ocean biogeochemical processes to rising concentrations of atmospheric CO_2 (e.g., Riebesell et al., 2007). With respect to the BCP, the use of mesocosm experiments would allow primary production and the formation, sinking, and decomposition of marine snow to be studied simultaneously for different food webs under otherwise identical conditions. These food webs could be based on different phytoplankton populations, contain different types or different abundances of zooplankton, and be exposed to different concentrations or different types of ballast minerals. Processes and interactions that had been identified in the laboratory as being pivotal to carbon flux, could then be investigated under more complex and slightly more natural conditions.

The goal of such experiments would be to quantify the relative fluxes of carbon, nitrogen, phosphorus and silicon, through various compartments of the food web versus incorporation into sinking particles under the different ecological conditions. This would enable demonstration of the key players and processes involved in BCPs of different overall capacity and efficiency. In addition, if a sufficient number of rates and fluxes between compartments of the food web are constrained during the experiments, this would provide data that could be used for the development and testing of process-oriented models of POC cycling and sinking in the upper ocean. This, in turn, would bring us closer to having a predictive understanding of the variability in the e-ratio and T_{eff} of the BCP at different times and places in the ocean.

Mesocosm experiments have proved particularly useful for investigating the fate of dust entering the upper ocean, in particular the balance of scavenging, solubilisation and export (Wagener et al., 2010; Bressac et al., 2012). The potential influence of iron on the BCP is returned to in Section 'Geochemical constraints on the extent and stoichiometry of production'.

In situ studies

There are also promising approaches for the study of marine snow from field samples and even in situ. The direct collection of particles for individual study using gel traps and marine snow catchers, to allow investigation of individual particle sinking speeds and composition, is increasing rapidly in popularity (Riley et al., 2012)). Another technique poised to have a major impact on our understanding of particle flux is the 'carbon flux explorer' (Bishop et al., 2004; Bishop, 2009). This is essentially an upward looking camera mounted on an Argo float which images particles as they settle onto the lens, and transferring these images in near real-time to a base station. It seems likely that the above techniques will transform our understanding of the spatial and temporal distribution of particle flux and the morphology of sinking particles in situ.

Zooplankton

The variety of copepod species/groups are likely to influence the vertical flux through very different mechanisms, due to their

differing feeding behaviour, metabolic rates and vertical migration. A natural way to approach this is by considering the copepods in two groups: large vertically migrating calanoid species such as *Calanus* spp., and small particle-colonising species, such as the poecilostomatoid copepod *Oncaea* spp. and the harpacticoid *Microsetella norvegica*. Previously, the cyclopoid *Oithona* spp. have also been considered to be an important flux feeder, due to its tendency for coprophagy (feeding on faecal pellets; Gonzáles and Smetacek, 1994). However, recent studies have failed to demonstrate any significant feeding of *Oithona* spp. on faecal pellets (Reigstad et al., 2005; Iversen and Poulsen, 2007), and its role in degrading the vertical flux appears to be less than previously thought. We will thus concentrate here on large calanoids and small particle-colonisers.

We assume that large calanoids consume particles in the surface layer at night, but descend during the day, to deeper in the water column where they respire and egest pellets. Small copepods, in turn, will not consume particles as a whole, but will colonise the sinking particles and stay attached, feeding and modifying the particle while it sinks through the water column. Whereas the effect of large copepods on vertical flux can be estimated by taking into account their diurnal feeding rate, vertical migration, gut evacuation time, respiration and pellet production rate (cf. Buesseler and Boyd, 2009), the effect of small copepods will depend on the species' ability to encounter and colonise a particle, and its residence time, feeding rate and pellet production on the particle (cf. Kiørboe, 2008). All of these processes are likely to be species-specific, and depend on a number of characteristics of the zooplankton and particles, as well as on diverse environmental factors (Table 3). At present we do not know the relative importance and interactions of these different processes or environmental variables in controlling the zooplankton consumption of sinking particles.

Research should be prioritised to reveal the proportional importance of different factors in controlling the zooplankton consumption and modification of flux, and to explain the consumption and/or modification of flux as a function of these important factors. A promising approach would be to improve the present estimates of particle feeding through direct measurements of individual physiological rates and additionally to assess the biochemical and mineral modification of the sinking particles. Below we give three specific examples of how this might be done. Such studies would considerably improve estimates of quantitative consumption and modification rates of the sinking particles by large versus small copepods (both in terms of carbon and of other properties). They would further allow these rates to be related to environmental conditions or specific characteristics of the zooplankton community and sinking particles.

Species-specific respiration rates

Typically, copepod consumption of sinking flux is estimated based on the size-fractionated biomass at different depths and on literature-derived body-size and temperature-specific respiration rates, which represent the minimum carbon consumption of metabolic needs (e.g., Steinberg et al., 2008). However, body-size specific respiration rates of particle-colonising species are likely to be lower than predicted based on the models. For instance, the specific respiration rates of *Oncaea* spp. are many times lower than those of similar sized calanoids (Nishibe and Ikeda, 2008), and mesopelagic copepods have lower respiration rates than epipelagic ones (Ikeda et al., 2006). As respiration rates are also influenced by, for example, feeding (Kiørboe et al., 1985) and swimming activity (Paffenhöfer, 2006), and as most calanoid copepods exhibit clear diurnal feeding rhythms (Saiz et al., 1999; Mayzaud et al., 2002), it is also likely that calanoid copepods have variable respiration rates at different depths and times of the day.

Direct measurements of individual day/night respiration rates of dominant species at different depths would thus be a relevant first step to improve the estimates of carbon demand of species. Combining respiration rates with egestion (pellet production) and growth / reproductive rates will give an individual carbon budget of the species, which can then be used to estimate the ingestion (as growth equals ingestion minus loss rates such as respiration, egestion and excretion). Individual carbon budgets, together with vertical day / night distribution profiles of zooplankton, will allow us to estimate where and how much carbon has been consumed by zooplankton, and where and how much of it has been respired or egested.

Feeding rates of particle colonising copepods

The feeding of copepods on sinking particles has been demonstrated both for large (Lampitt, 1992; Lampitt et al., 1993) and small (Alldredge, 1972) crustaceans, but rarely quantified. At present, it is assumed that feeding on aggregates can consume a significant part of the vertical flux (Kiørboe, 2000; Koski et al., 2005; Steinberg et al., 2008), but we do not know how the feeding rate of different species is influenced by aggregate type or its characteristics (see Table 3). Preliminary studies show that phytoplankton aggregates and appendicularian houses induce different encounter rates and handling times for a harpacticoid copepod (*M. Koski, F. Lombard*, unpubl. data). While phytoplankton aggregates are encountered at a higher rate, appendicularian houses provide food faster. Measurements on functional responses of feeding on different types of aggregates by the dominant copepod species would provide direct estimates of encounter rates, handling times and maximum ingestion rates, as a function of aggregate characteristics. These measurements would improve our understanding of the factors controlling consumption rates, and could be used to verify the magnitude of consumption rates obtained indirectly via respiration and growth measurements.

Modification of sinking particles by zooplankton

Zooplankton activities modify sinking particles due to both physical fragmentation and feeding (Wilson et al., 2008; Wilson and Steinberg, 2010). However, until recently research has focused on the effect of zooplankton activities on the total carbon export, and less on the qualitative changes in sinking particles. In the conceptual framework described earlier, large copepods would consume the particle as a whole, and produce another particle (faecal pellet) at a different depth, while small copepods would continuously modify the particle as it sinks through the water column. Although no direct measurements of the changes in aggregate quality due to zooplankton processes exist, the larger and older aggregates typically have a higher C:N ratio than smaller aggregates (Alldredge, 1998) and ageing aggregates are quickly depleted in short-chain fatty acids (Balzano et al., 2011). Zooplankton growth and reproduction need essential elements, for instance nitrogen (Kiørboe, 1989), polyunsaturated fatty acids (Jónasdóttir et al., 2009) and sterols (Klein Breteler et al., 2005), which cannot be synthesised *de novo* and have to be derived from the food. It is thus likely that the zooplankton activity (feeding or assimilation) would selectively remove the most nutritious elements, so that the resulting pellet or older aggregate would have a higher C:N ratio and lower content of, for example, polyunsaturated fatty acids than the original aggregate.

Geochemical constraints on the extent and stoichiometry of production

An alternative approach to *in vitro* and *in situ* observations in studies of biological production rates and the Biological Carbon Pump is the analysis of temporal signals of nutrient and carbon

Table 3
Overview of some of the processes involved in copepod-aggregate interactions and the main environmental variables affecting them. For references on zooplankton bioenergetics and its dependence on environmental factors, behaviour, feeding and aggregate fragmentation, see, for instance Kiørboe et al. (1985), Dilling and Alldredge (2000), Besiktepe and Dam (2002), Saiz and Calbet (2007) and Kiørboe (2008).

	Zooplankton	Sinking particle	Environment
Encounter rate	Swimming velocity	Sinking (size, ballast), concentration, chemical 'trail'	Food-web structure, productivity, turbulence, hydrography
Residence time	Swimming ability Preferred habitat (benthic/semi-benthic/pelagic)	Quality (origin, size) concentration, resident colony	Food-web structure, productivity, predation, resuspension
Feeding rate	Body size, metabolic rate, selection, hunger	Quality (origin, size, ballast, TEP), concentration	Food-web structure, productivity, temperature
Fragmentation	Swimming velocity, feeding	Size, concentration, quality	Food-web structure, productivity, turbulence
Repackaging	Feeding, assimilation efficiency	Size, quality (e.g., mineral content)	Food-web structure, productivity, turbulence, temperature
Active transport	Vertical migration, respiration, egestion, gut passage time, mortality	Concentration, quality	Water column depth, productivity, predation, temperature

utilisation and release. The approach has been used to identify the (de)coupling of carbon–nitrogen–phosphorous cycles in the open ocean during dedicated process studies (Sambrotto et al., 1993; Koeve, 2006), deliberately perturbed systems (e.g. Bozec et al., 2005) time-series analyses (Bates et al., 1996; Falck and Anderson, 2005) and basin-scale database analyses (Körtzinger et al., 2001; Koeve, 2006). It has also been successfully applied to mesocosm studies to investigate the effects of ocean acidification (Bellerby et al., 2008)

Iron

Iron strongly influences a variety of surface biogeochemical processes in the oceans, including nitrate uptake, nitrogen fixation and photosynthesis. These processes, and the BCP which is strongly influenced by them, are therefore susceptible to variability in the supply of iron.

In the southern part of the North Atlantic a large supply of dust enters westwards from the Sahara, with a fraction making it all the way across the basin (Prospero et al., 2010). Although dust may directly influence the BCP by providing ballast for sinking material (Section 'Particle sinking'), a major indirect influence is as an important conduit for the transfer of iron to the ocean. Because the input of iron via dust deposition is concentrated in the subtropical North Atlantic, the primary beneficiaries of this source are diazotrophic nitrogen fixers, well adapted to the stable water column and relatively high temperatures. Although nitrogen fixation within the Atlantic is strongly spatially correlated with the areas of highest dust deposition (Monteiro et al., 2011), incubation experiments to address this hypothesis have been somewhat ambiguous, potentially due to the low density of nitrogen fixers in the upper water column where N fixation takes place. Nitrogen fixation in the southwest North Atlantic is probably additionally influenced by the Amazonian outflow, which transports nitrogen northward across the equator (Subramaniam et al., 2008). Focusing on the BCP, the fate of nitrogen fixers is an outstanding question. The existence of elevated N/P in the thermocline could be indicative of remineralisation of sinking diazotrophic material in the mesopelagic zone (100–1000 m), although there are several other mechanisms which could result in excess nitrate in the subtropical North Atlantic (Hansell et al., 2008). Although one explanation is that this material has simply been repackaged, recent observations of nitrogen fixing taxa in the thermocline and at abyssal depths indicate that some fraction of this material is exported directly (Subramaniam et al., 2008; Karl et al., 2012).

At high latitudes there is little deposition of Saharan dust, though surface (Prospero et al., 2012) and, less frequently, volcanic (Achterberg et al., 2013) sources in Iceland exist. In this sector of the North Atlantic the vertical transport of nitrate rich waters that are iron poor relative to planktonic nutrient requirements may result in iron limitation of nitrate assimilation and photosynthesis.

The observed subsequent subduction of large volumes of water rich in unused nutrients, which occurs here during North Atlantic Deep Water formation, represents an inefficiency in the BCP which enhanced iron supply at high latitudes might eliminate. Thus the potential role of iron at high latitudes, particularly in the context of a changing climate, should not be ignored.

Stoichiometry

Temporal signals of net stoichiometry provide absolute net community values for carbon and nutrient utilisation for a prescribed timescale. During the early stages of a spring bloom, with low heterotrophy, the analyses can approximate new production and overall the response over a bloom or season can be considered to approximate net community production. Changes in the net stoichiometry may highlight regions and depths of preferred production and respiration. Decoupling of the signals has been used to indicate preferential respiration and regions of export. These are useful for model-data comparisons where whole ecosystem integrated performance analyses identify where models are performing optimally and can thus highlight, through sensitivity analyses, the dominant ecosystem or biogeochemical process(es) for a particular region and season. The approach requires that the model has a flexible cell quota to allow for flexibility in elemental stoichiometry (e.g. Vichi et al., 2007; Allen et al., 2001; Omta et al., 2006).

Empirical algorithms for flux attenuation

The work of the Vertigo field programme in the Pacific provides compelling evidence that significant spatial variability exists in the rate at which sinking organic matter is degraded (Buesseler and Lampitt, 2008). Given the strong seasonal cycle inherent in the BCP, it seems sensible to assume that there is also considerable temporal variability. Kwon et al. (2009) have shown, using numerical models, that air sea partitioning of CO_2 can be sensitive to relatively small changes in the rate at which exported sinking material is remineralised. We therefore need to be able to predict how the vertical attenuation of flux varies both spatially and temporally if our ambition to model the future evolution of biological carbon sequestration is to be achieved.

In the longer term, such predictions need to be possible using the parameters and processes present in the ecological component of the global mechanistic models used for climate studies. The likely range of 'predictors' available in our future models is the topic of some debate, touched on in Section 'Modelling'. However, ones that have all already been included and would be of considerable use for this task include size structure, the production of fast and slow sinking detrital pools, differential grazing and the presence of biominerals. A mechanistic model that accurately describes the fate of organic material as it sinks is still a long way in the future, however, and so more immediate, pragmatic, approaches

are required, which will also help construct the future mechanistic models.

Regression analysis is a powerful way of extracting first order relationships that reveal how natural variability in attenuation is linked to potential environmental factors and indices of ecosystem structure and functioning such as oxygen abundance, temperature, primary production and biomineral concentration. We therefore advocate repeated simultaneous observations of attenuation alongside such parameters. However, such observations are time consuming and technologically challenging to make and in parallel we feel that more effort should be focussed on how the vast archive of profiles of particle concentration and characteristics (which are much easier to collect) could be systematically converted to estimates of sinking flux. This would potentially vastly expand the calibration data available to develop empirical algorithms. Recent theoretical and computational developments (Lam et al., 2011; Guidi et al., 2008) suggest that there may be some ground for optimism. However, this is a formidable task. Not least is the difficulty involved in separating out the two processes of remineralisation and sinking from 'snapshots' of the material at each depth. A major part of this difficulty arises from the paucity of independent estimates of heterotrophic activity in the interior. A variety of techniques, including allometry and radiotracer methods, now exists to address this and should be pursued. Wherever this has been attempted it has largely failed, a factor which is often ascribed to the inadequacy of the data used. However, extending the approach into different vertical regions may be an important development.

Modelling

As outlined above, the BCP represents many interconnected processes from primary production, the microbial loop, particle aggregation and sinking, remineralisation, grazing and vertical migration to the physical transport of material by ocean currents. The modelling challenge is to synthesise knowledge of these processes in a quantifiable and dynamic manner to provide accurate estimates of the sequestration flux of carbon to the deep ocean resolved at a regional and seasonal level; estimates that can be coupled to global biogeochemical models. However, models serve an important secondary purpose in that they provide a scientific tool. That is, they provide a framework wherein hypotheses related to the various interconnected elements of the BCP can be formulated and tested.

The important conceptual development of trait-based models appears to be a particularly fruitful avenue in addressing marine ecosystem processes. Such models avoid the architectural restrictions of functional group models, allowing ecosystem structure and biodiversity to emerge though evolutionarily consistent mechanisms. These "self-organising" models are beginning to be applied in the field of marine biogeochemical modelling (e.g. Follows et al., 2007; Bruggeman and Kooijman, 2007).

Primary production and export flux

The availability of light and nutrients are the key factors influencing primary production. However, not all phytoplankton have the same requirements and there is a constant competition between species that have adopted different trade-offs in their growth physiology. Key trade-offs include the relative investment in light harvesting apparatus, nutrient uptake sites, and grazing defence. A key attribute that reflects these trade-offs is the large intra- and inter-species variation in elemental composition exhibited by phytoplankton, with high organic N:P ratios frequently observed in oligotrophic marine environments, and lower values found in regions were nutrients are more abundant (e.g.

Copin-Montegut and Copin-Montegut, 1983; Downing, 1997; Körtzinger et al., 2001). Within this context, the application of trait based modelling has led to theoretically predicted stoichiometries (Klausmeier et al., 2004), from which the composition of the phytoplankton community can be seen to emerge from prevailing light and nutrient conditions (e.g. Merico et al., 2009).

Zooplankton grazing, respiration, and excretion, coupled with vertical migration behaviour, also play a pivotal role in ocean biogeochemical processes, including nutrient cycling, and carbon flux and sequestration to the deep ocean (Steinberg et al., 2001; Legendre and Rivkin, 2005; Jackson and Checkley, 2011). The concept of adaptive behaviour is a modelling tool that can be applied here. Namely, rather than use empirically derived parameters to simulate vertical migration, we can treat vertical migration as an emergent behaviour arising from a trade-off between the benefits, costs and risks (in terms of fitness) associated with specific migration strategies (Fiksen and Giske, 1995); an evolutionarily consistent behaviour that can thus adapt to prevailing conditions.

Dissolved organic matter is by far the largest pool of organic matter in the sea comprising ~97% of all organic carbon (Hansell and Carlson, 1998), and is roughly equal to the amount of carbon in the atmosphere. While generally regarded in models as a large inert reservoir, studies have revealed that DOM is an active and dynamic component in carbon biogeochemical cycles and plays important roles in marine ecosystems and BCP (e.g. Mopper et al., 1991). At the sea surface, photochemical reactions involving DOM (Bushaw et al., 1996) produce inorganic carbon, low-molecular-weight organic compounds, trace gases, and phosphorus- and nitrogen-rich compounds (e.g. Vähätalo and Zepp, 2005; Stedmon et al., 2007). In the pelagic and twilight zones DOM is an important element of the microbial loop (Suttle, 2007). In addition to carbon, DOM also contains macro-nutrients (Bronk, 2002; Benner, 2002) and a raction of labile organically bound N and P can be directly assimilated by bacteria and in some cases phytoplankton (Bronk, 2002). However, a considerable fraction is bound in more refractory compounds and not rapidly available. Biotic and abiotic remineralisation processes gradually degrade this material and release bioavailable forms of N and P (Moran et al., 2000; Vähätalo et al., 2003). The susceptibility of DOM to degradation depends on its chemical composition and therefore ultimately its source. Several modelling studies (e.g. Moloney and Field, 1991; Anderson and Williams, 1998; Vallino, 2000) suggest that inclusion of dissolved organic nitrogen cycling in ecosystem models can have important implications on the regulation of nutrient cycling, while the dynamics of the global dissolved organic carbon pool remains an open modelling question.

Flux attenuation and sequestration

Particle transformation in both the surface and subsurface ocean sets the magnitude of POM export (Azam, 1998; Boyd and Stevens, 2002), and recent models incorporate food-web structure (e.g., Laws et al., 2000) and particle transformations (e.g., Moore et al., 2002b). However, few modelling studies have evaluated the relative importance of particle transformations to export flux, where both mesozooplankton and bacteria play an important role (Boyd et al., 1999). Difficulties in ranking the many particle transformation processes may stem from some processes being specific to particular water masses or exhibiting seasonality. While some modelling studies have provided insights into specific aspects of these processes (Jackson and Burd, 2001; Boyd and Stevens, 2002), a priority is to develop an integrated modelling framework that can accommodate and test the contribution of these various processes to the net flux attenuation as a function of geographic location and season.

Modelling approaches and synthesis

Finding the appropriate level of complexity that will enable ecosystem models to have most skill in predicting biogeochemical fluxes is a fundamental problem. Recent results suggest that models based on PFT (e.g. ERSEM Blackford et al., 2004) are more responsive than a NPZD (e.g. Fasham et al., 1990) model to the simulated environment in which they are placed and that they produce a more extensive range of emergent properties (Sinha et al., 2010). However, the question of how real these responses are remains, and further data is required to resolve this issue. Since there is no consensus on how many PFTs are needed to represent which key processes, flexibility in approach is needed in order to select appropriate levels of complexity, depending on the question, geographical area, or research agenda. Likewise, the model representation of the microbial loop, and compartmentalisation of organic nutrients can have implications for the fidelity of models (e.g. Hood et al., 2001; Spitz et al., 2001; Anderson and Pondaven, 2003; Salihoglu et al., 2008).

The approach that we suggest is to construct model frameworks in which models of different complexity can be compared. There are already techniques being developed and applied that are providing considerable insight into this issue of the how complex a model needs to be, for example using techniques to accelerate global models (e.g. Khatiwala, 2007; Khatiwala, 2008; Kriest et al., 2012; Kriest and Oschlies, 2008) and to systematically decompose complex models into simpler ones (e.g. Ward et al., 2013).

Additional comparison should be made using agent-based and trait-based models, particularly in the context of research tools. One of the central challenges of biological pump modelling is that material (e.g. carbon and nutrients) undergo continual phase changes, from dissolved to particulate (both living and dead) and back to dissolved. This effectively decouples and recouples material from the ocean circulation at various stages throughout its cycle. This is compounded by the fact that many of the important processes that govern the export and sequestering fluxes involve particle–particle interactions (e.g. the coagulation of detritus and its colonisation by microbes and zooplankton). Agent-based models provide a natural platform through which these varied processes and their interconnections can be examined. The feasibility of this approach has been considerably advanced recently by the development of direct *general-purpose computation on Graphics Processing Units* (*GPGPU*), dramatically increasing the efficiency of large agent-based models. One advantage of agent-based models is that the variation of traits within a community can be introduced in a transparent manner. Not all agents of the same class need be identical, and success of variant traits can be assessed through a fitness metric (e.g. the ratio of the rate at which organic carbon is assimilated to the mortality rate integrated over a suitable time horizon) and can be applied to both physiological traits (e.g. nutrient affinity) as well as behavioural traits (e.g. foraging strategy). The overall aim is to provide mechanistic descriptions of the various component processes comprising the BCP, as well as the integrated effect in exporting and sequestering carbon

in the ocean. A summary of the specific processes we suggest should be targeted for detailed modelling studies are listed in Table 4.

Conclusions

Much uncertainty remains concerning the BCP in the North Atlantic. Estimates from a variety of methods, collated here, indicate an export of approximately 1 Gt C yr^{-1}, but range over a factor of two either side of this. Furthermore, direct data for how this key flux varies spatially within the North Atlantic and temporally through the seasonal cycle are still rare. For example, even at well-studied sites like BATS, PAP and ESTOC it is still impossible to separate out the influence of seasonal, inter-annual and spatial variability. While much work remains to be done in providing a robust baseline of information on the BCP, it is also important to focus efforts on the processes which control the BCP, phenomena such as aggregation dynamics, plankton interactions and others described in this review. An improved mechanistic understanding is key to any ability to predict changes in the BCP under proposed future scenarios. The requirement, therefore, is unsurprisingly for a co-ordinated and multidisciplinary range of approaches. As an example of this, the EU-funded EuroBASIN programme, involving researchers from across Europe, is using a combination of focussed laboratory work, mesocosms, fieldwork, data-mining and modelling to tackle this fundamental problem. With an ambitious field programme and schedule of work this programme clearly has the potential to improve our understanding considerably. However, given that we are still some way from being able to account, even to first order, for what happens to all of the carbon that passes in organic form through the top 1000 m of the North Atlantic, one of the most heavily studied regions of the world's oceans, much remains to be done. It is hoped that this review gives an indication of the most important and fruitful topics to pursue as well as the incentive to pursue them.

Acknowledgements

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Table 4
The processes that further modelling studies should consider. Suggestions for specific measurements needed for models are given in italics.

Algal community structure
Algal aggregation
Ballasting (enhancing sinking rates e.g. diatoms, coccolithophores)
Particle aggregation (e.g. detritus)
Temperature dependent decomposition of particulate and dissolved matter by bacteria
Preferential remineralisation of P, N, Si (versus C)
Vertical migration and active transport by zooplankton
Fragmentation and repackaging of detrital material by mesozooplankton

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