



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 (CO₂) sink, dominating the terrestrial and atmospheric reservoirs, and absorbing more than a quarter of anthropogenically released CO₂ (Sabine et al., 2004). It has been estimated that pres-

ent day atmospheric CO₂ 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 CO₂ in the atmosphere due to anthropogenic processes (3.2 Gt C) and five times larger than the annual net flux of CO₂ 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 CO₂ partitioning (Rost et al., 2008). These changes might occur due to climatically driven effects, such as increases in atmospheric and oceanic CO₂ 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 Garçon, 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; Raitos 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 $\sim 400 \text{ mg m}^{-2}$ at 18°N to $\sim 3000 \text{ mg m}^{-2}$ 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 ($\sim 1 \text{ mm}$) 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 diel 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 (~ 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

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