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UNDERSTANDING THE ROLE OF THE BIOLOGICAL PUMP IN THE GLOBAL CARBON CYCLE

An Imperative for Ocean Science

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Anthropogenically driven climate change will rapidly become Earth's dominant transformative influence in the coming decades. The oceanic biological pump—the complex suite of processes that results in the transfer of particulate and dissolved organic carbon from the surface to the deep ocean—constitutes the main mechanism for removing CO_2 from the atmosphere and sequestering carbon at depth on submillennium time scales. Variations in the efficacy of the biological pump and the strength of the deep ocean carbon sink, which is larger than all other bioactive carbon reservoirs, regulate Earth's climate and have been implicated in past glacial-interglacial cycles. The numerous biological, chemical, and physical processes involved in the biological pump are inextricably linked and heterogeneous over a wide range of spatial and temporal scales, and they influence virtually the entire ocean ecosystem. Thus, the functioning of the oceanic biological pump is not only relevant to the modulation of Earth's climate but also constitutes the basis for marine biodiversity and key food resources that support the human population. Our understanding of the biological pump is far from complete. Moreover, how the biological pump and the deep ocean carbon sink will respond to the rapid and ongoing anthropogenic changes to our planet—including warming, acidification, and deoxygenation of ocean waters—remains highly uncertain. To understand and quantify present-day and future changes in biological pump processes requires sustained global observations coupled with extensive modeling studies supported by international scientific coordination and funding.

BACKGROUND

The pelagic and coastal oceans, together with the Great Lakes, contain over 90% of Earth's bioactive carbon (bio-C) and exert a major influence on the global environment by modulating fluxes and transformations between various carbon reservoirs. In particular, the ocean's bathypelagic zone (including abyssopelagic and hadalpelagic zones) is by far the single largest inventory of bio-C on Earth. It contains 3,150 Pmol (Pmol = 10^{15} mole; Figure 1), more than 50 times greater than the amount of CO_2-C in the atmosphere, currently estimated to be about 62.5 Pmol (pre-industrial levels are estimated to have been about 48.3 Pmol; IPCC, 2007), and more than an order of magnitude greater than all the bio-C held in terrestrial vegetation, soils, and microbes combined. The sink-strength (or "feedback efficiency"; Falkowski et al., 2000) of this reservoir is critical in buffering Earth's atmosphere from a rapid CO_2 increase. Operating in parallel, the inorganic gas-exchange pump (which includes the carbonate/bicarbonate buffer-driven solubility pump) is estimated to account for only ~ 10% of the total transfer of dissolved inorganic carbon (DIC) from surface to deep waters in the modern ocean (e.g., Sarmiento and Gruber, 2006). In this article, we exclusively focus on the biological pump.

The biological pump starts in the

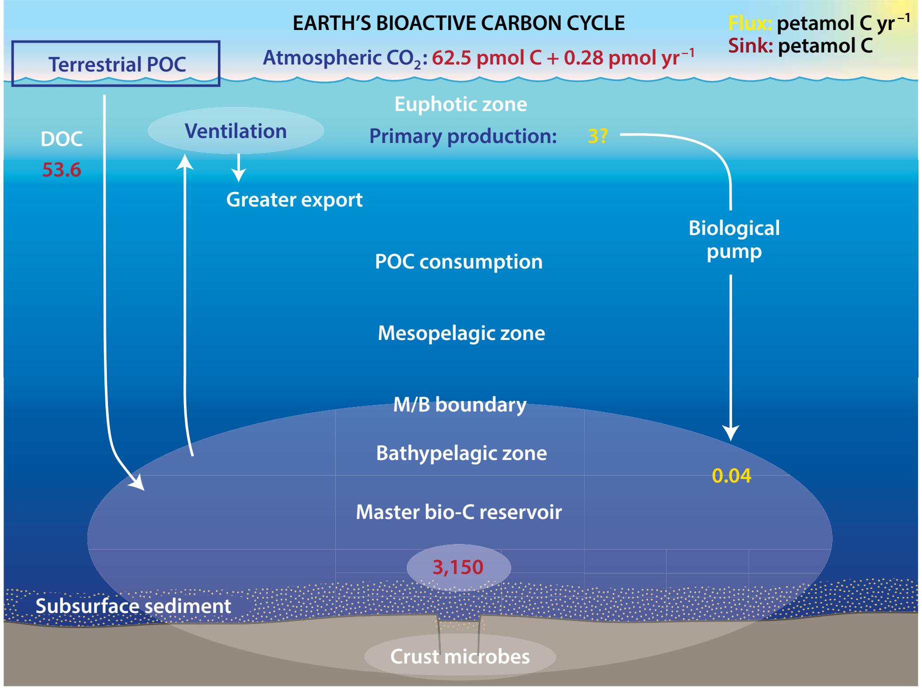

Figure 1. A simplified conceptual diagram of Earth's bioactive carbon cycle with the size (petamol C) of the atmospheric reservoir as CO_2 (CO_2-C). The deep ocean sink is shown in red, and key fluxes (petamol C yr^{-1}) are in yellow. The current CO_2-C inventory in Earth's atmosphere (62.5 petamol C) is increasing at the rate of 0.28 petamol C yr^{-1}. POC (particulate organic carbon) exported to the bathypelagic zone by the biological pump is estimated at 0.04 petamol C yr^{-1}. This zone, containing 3,150 petamol C, represents Earth's master reservoir of bioactive C. For clarity, the solubility pump, which is estimated to account for ~ 10% of the total transfer of DOC (dissolved organic carbon) from surface to deep waters in the modern ocean (Sarmiento and Gruber, 2006), is not included. M/B = mesopelagic/bathypelagic.

euphotic zone with the photosynthetic fixation of inorganic carbon into phytoplankton biomass. Current estimates of global oceanic primary production (G-PP) are between 3 and 4 Pmol C yr^{-1} (e.g., Berger, 1989; Antoine, 1996; Behrenfeld and Falkowski, 1997; Chavez et al., 2011). Research undertaken during the US Joint Global Ocean Flux Study (US JGOFS, ca. 1987–2005) and subsequent programs clarified that a fraction of this bio-C is rapidly removed from surface waters and exported to the ocean's interior in the form of particulate organic matter (POM) through a complex interplay of biological processes combined with gravity (eco-dynamic transport; e.g., Honjo et al., 2008; Online Supplement, Section 1). Chemoautotrophic processes in the meso- and bathypelagic realms may also play important roles in modulating deep ocean carbon inventories (e.g., Arístegui et al., 2009; Swan et al., 2011; Online Supplement, Section 2).

Prior studies suggest that the annual flux of bio-C to the bathypelagic ocean by direct transport of POC is ~ 0.04 Pmol yr^{-1} (Figure 1; Honjo et al., 2008). Notably, this flux represents only 14% of the current annual increase of carbon as atmospheric CO_2, highlighting the importance of understanding how the biological pump will respond to increasing atmospheric CO_2 concentrations, and whether the bathypelagic carbon reservoir can remain a sink for this anthropogenic carbon.

There are serious deficiencies in our ability to place these processes in a quantitative context, to determine their dynamics, and to assess how the ocean will respond to, or exacerbate, climate change, pollution, and over-exploitation of marine resources. For example, our recognition of the large stock of prokaryotic biomass throughout the ocean and in subsurface and subseafloor environments (e.g., Whitman, et al., 1998; Arístegui, et al., 2009; Lauro and Bartlett, 2008; Kallmeyer et al., 2012) and of dissolved organic carbon residing in ocean waters (Hansell and Carlson, 2013) sharply contrasts with our limited knowledge of their roles in biogeochemical processes. A complete mechanistic and quantitative understanding of the biological pump is essential for determining its importance in modulating atmospheric CO_2 and predicting its future behavior. Programs such as the Global Carbon Project (http://www.globalcarbonproject.org) as well as other global carbon flux modeling efforts are in need of far more extensive and comprehensive ocean data to further refine their predictive capabilities. Input from this community will be critical in guiding the prioritization for measurements needed to address current deficiencies in our models.

ADDRESSING KNOWLEDGE GAPS: THE GRAND CHALLENGE

Current global flux estimates of bio-C generally stem from data acquired from highly diverse and often asynchronous observations. There is considerable uncertainty in these estimates due to sparse and heterogeneous data coverage that may fail to capture seasonal variability or incorporate geographical biases. For example, although US JGOFS provided a wealth of new insights, derivation of global-scale carbon fluxes from this and other programs is fraught with uncertainty because discontinuous observations spanned > 10 years and various parameters were not measured simultaneously. These deficiencies reflect both a lack of technology and limited opportunities for ocean observations of the type and scope required to develop precise constraints on the biological pump on temporal and spatial scales suitable for assessing links and sensitivity to global change.

SPATIAL AND TEMPORAL VARIATIONS IN BIO-C CYCLING

In the euphotic zone, or "phytoplankton domain," accurate constraints on marine primary production must be established in terms of absolute flux, photoautotrophic community structure, and biomineral (ballast) production and removal rates. Satellite-based surface ocean color observations have yielded the most spatially comprehensive view of G-PP (e.g., Behrenfeld and Falkowski, 1997) and will be indispensable in future ocean observing efforts. However, these measurements probe only the surface layers of the euphotic zone and presently deliver only restricted information on the diversity of primary producers (e.g., Alvain et al. 2005; Bracher et al., 2009) and on the fate of this photosynthetically derived carbon. While new constraints on organic carbon export are being realized through coupling of satellite observations with food web models (Siegel et al., 2014), high-resolution time-series measurements (e.g., Taylor and Howes, 1994) would provide greatly improved assessment of carbon and biomineral production throughout the euphotic zone and of autotrophic processes at all ocean depths (Figure 2).

In the mesopelagic zone, or "prokaryote/zooplankton domain," both prokaryotic and eukaryotic organisms are understood to strongly influence biogeochemical processes. However, their impacts on the net flux and composition of settling particulate organic carbon (POC), and of dissolved organic carbon (DOC), remains poorly constrained (e.g., Steinberg et al., 2002; Buesseler et al., 2007). In particular, the diel vertical shuttling of zooplankton through the mesopelagic zone (e.g., Angel and Baker, 1982) involves complex ecodynamic transport and transformation of POC (Figure 2), imposing serious challenges to the characterization and parameterization of this important but elusive component of the biological pump. Microbes occur abundantly in mesozooplankton guts (e.g., Gowing and Wishner, 1998), free settling fecal pellets (Honjo, 1997) and marine snow (e.g., Alldredge and Cox, 1982; Alldredge and Silver, 1988). Quantitative research on these microbes is greatly needed for understanding the transport of bio-C throughout the water column (Online Supplement, Section 3).

The bathypelagic zone or "prokaryotic domain" comprising Earth's bio-C master reservoir (Figures 1 and 2) is crucial in the context of the oceanic carbon cycle, yet it remains grossly undersampled. The metabolic activity of prokaryotic/eukaryotic communities largely controls in situ organic matter remineralization to ΣCO_2-aq in the bathypelagic water column and underlying sediment because of the scarcity of zooplankton in this zone. Globally, the amount of prokaryote biomass in subsurface ocean sediments remains a topic of debate. The standing crop of bio-C in subsurface sediment is estimated to be 25 Pmol C (40% of the amount of current atmospheric CO_2-C) and includes diverse assemblages of microorganisms (Whitman et al., 1998; Kallmeyer et al., 2012; Figure 1). Further research is necessary to elucidate and quantify rates of carbon transformation in bathypelagic waters and underlying sediments.

The dynamics of ocean margin ecosystems and associated bio-C are even more complex than pelagic ocean dynamics. The margins are regions of large ecological diversity (Levin and Sibuet, 2012) and of high carbon productivity, export, and burial (Tsunogai

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et al., 1999; Thunell et al., 2000; Muller-Karger et al., 2010; Montes et al., 2012). Characterizing processes on the continental margins and their influence on deep ocean bio-C inventories is therefore a prerequisite for developing a complete understanding of the global carbon cycle, yet ocean margins remain woefully underrepresented in global carbon databases and models (e.g., Thunell et al., 2007).

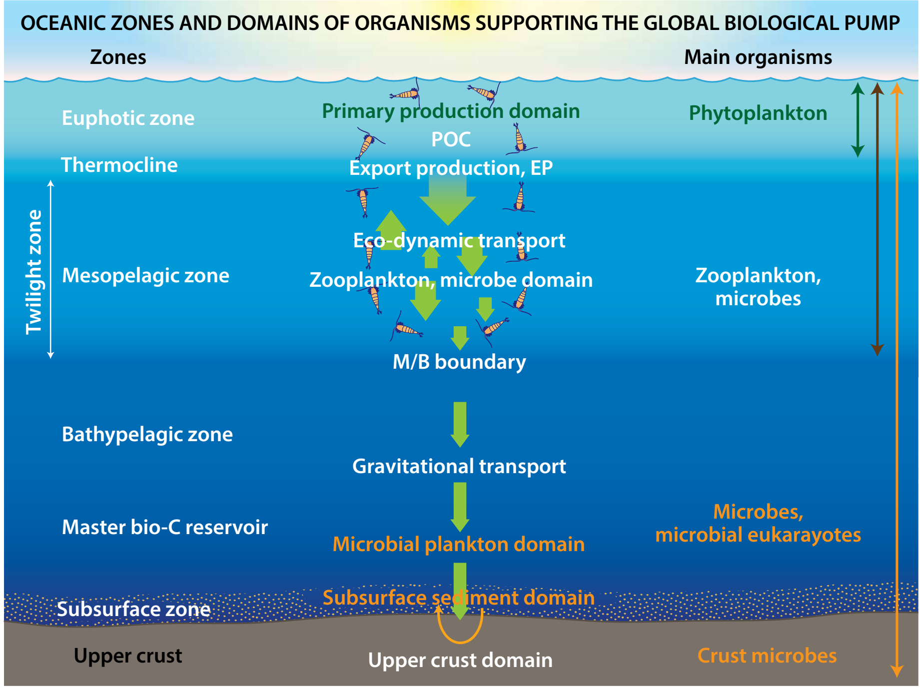

Figure 2. Schematic illustration of major oceanic zones and biological domains between the air-sea interface and the deep ocean floor, including the subsurface zone. Below the mesopelagic/bathypelagic (M/B) boundary, there is little zooplankton activity, so, hypothetically, the large population of prokaryotes near the bottom of the water column is supported by gravitational transport of biomineral-ballasted particles that descend from surface waters.

THE GLOBAL BIOGEOCHEMICAL FLUX OBSERVATORY CONCEPT

The rapid pace of atmospheric carbon accumulation is likely to increase as a result of positive feedback mechanisms: ocean warming, deoxygenation, and acidification are proceeding at measurable rates and on a global scale. Assessment of the impacts of these and other perturbations related to global climate change on ocean biogeochemical processes can only be addressed via sustained observations (e.g., Wunsch et al., 2013). Linking changes in the physical/chemical environment with biological and biogeochemical properties and processes and accurate modeling and prediction of the effects of global change (e.g., Siegel, et al., 2014) requires scientists across multiple ocean research disciplines to develop and build upon technological innovations toward cost-effective implementation of reliable systems. It is also important to instill in society appreciation of the ocean as a vital global resource, understanding of its role in maintaining the habitability of our fragile planet, and recognition of the need for multidecadal observations of ocean processes.

The Global Biogeochemical Flux Observatory (GBF-O) concept offers a framework for implementing a sustained observation and sampling program that complements elements of the US Ocean Observatory Initiative (OOI) and other ocean observatory programs (e.g., http://www.oceansites.org, http://www.ioc-goos.org), as well as other observational approaches, such as satellite-based global investigations of marine primary productivity (Behrenfeld and Falkowski, 1997), shipboard time-series programs (Church et al., 2013), and widespread dissemination of floats and gliders equipped with sensors for constraining ocean biogeochemical processes (Johnson et al., 2009). The GBF-O concept is based on a combination of established technologies and advanced autonomous instrumentation operated synchronously. Among the key facets of the GBF-O that distinguish it from the OOI are an emphasis on long-term sample acquisition, preservation of the samples for subsequent retrieval of maximum biogeochemical (e.g., genomic) information, and return of the samples for detailed laboratory-based analyses (Online Supplement, Section 3). These elements are vital for extracting the greatest level of information and for developing a sample legacy that will be invaluable for future research as new analytical technologies emerge.

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Methodology

Key methodological elements of the GBF-O concept are:

1. Observations from the air-sea interface through the euphotic, mesopelagic, and bathypelagic zones to the seafloor
2. Sustained, synchronized time-series observational modes to monitor the seasonal and interannual rhythms of the biological pump
3. Ecosystem characterization encompassing a broad spectrum of organisms from pelagic to benthic communities, and from prokaryotes to zooplankton
4. Implementation and maintenance of centralized laboratories for accurate and precise determination of core biogeochemical flux parameters
5. Incorporation of profiling and fixed-depth contextual instrumentation
6. Construction of a long-term archive that acquires and preserves samples for future in-depth "omics" and related studies associated with biogeochemical and paleoceanographic proxy research (Online Supplement, Section 2)

Technical Readiness

The challenges of implementing the GBF-O approach are formidable, but they must be met in order to fully understand the workings of the biological pump and associated processes in the context of global change. Autonomous observation of ocean properties represents a major new emphasis within the ocean science community (e.g., Johnson et al., 2009; Bishop, 2009), and remote observation capabilities are continuously being developed. Mooring systems that support full ocean depth biogeochemical experiments also have advanced during US JGOFS and related programs. As for any observatory, it is essential that all of the associated instruments and supporting materials be designed and manufactured to produce consistent results. Mass production of instruments and mooring platforms is crucial to ensure broad availability of serviceable, cost-effective systems that meet rigorous specifications.

Orchestration of GBF-O Arrays

Synchronization of instruments and sensors within and between observatory arrays is critical for understanding the rhythms of global ocean biogeochemical processes. The majority of POC (often 70% to 90% of annual export) and other biogenic particulates are produced during episodes that usually occur only once or a few times a year in response to seasonal phytoplankton blooms (e.g., Wefer et al., 1988). The resulting sharp export pulses gradually diminish in amplitude with depth (reviewed in Honjo et al., 2008). Defining the annual pattern and evolution of this curve throughout the water column represents an important aspect of constraining the functioning of the biological pump and its impact on ocean-atmosphere carbon balances (Kwon et al., 2009).

Preliminary Vision for GBF-O Implementation

Figure 3 presents one vision of a stand-alone GBF-O instrument. Although dependent upon local bathymetric conditions, the moorings within the array would typically be set from several to 12 nm apart (to allow for unobstructed deployment). Each mooring would be kept in vertical alignment by a single syntactic-foam sphere with the appropriate buoyancy. In this example of a GBF-O array, samplers are deployed at specific intervals along each mooring to cover different water column domains. Such an array could host more than 25 major time-series devices as well as many contextual sensors and "guest" instruments. Further details of the GBF-O array and instruments are in the Online Supplement, Section 4.

A single array of this type, equipped with the instrumentation capabilities depicted in Figure 3, would yield a wealth of new information. Deployment of multiple arrays throughout the major ocean basins would form the basis for a GBF-O. Selection of specific locations for array deployments would be based on multidisciplinary perspectives and consensus in order to maximize our level of understanding and predictive capability regarding biological pump processes. Criteria for determining array locations would, for example, involve assessments of primary production based on ocean color (e.g., Behrenfeld and Falkowski, 1997), ocean biogeochemical provinces (e.g., Longhurst et al., 1995), observations from prior studies (e.g., Honjo et al., 2008), bathymetric variations, and maritime logistics.

CONCLUSION

Our ability to model the workings of the oceanic biological pump comprehensively and accurately is a critical component of global efforts to forecast the trajectory and effects of anthropogenic climate change. We have begun to understand the major features of the biological pump and its key role in the sequestration of carbon in the ocean, but we are still blind to many of its characteristics and far from developing comprehensive mechanistic and quantitative constraints on its myriad processes. Assessment of the impact of climate change on ocean biogeochemical processes and ecosystems, and vice versa, can only be addressed via global, standardized, sustained, synchronous observations over coming decades. Indeed, we hope to galvanize the oceanographic community to champion the need for a century of ocean observation—deploying a truly global array of state-of-the-art sensors and other instrumentation that will be necessary for understanding not only carbon flow in the ocean but also all of the ocean's intimately related inhabitants.

Recent rapid progress in underwater technologies, particularly ocean robotics and novel in situ sensors, experimentation platforms, and discrete samplers, has made it feasible to develop high-endurance sentry instruments capable of operating in diverse ocean environments to provide these essential data. However, the magnitude of the undertaking will require international scientific coordination and funding. We must strive as a community to integrate all emerging ocean observatories to forge the best possible global planetary observation network and elevate its priority above that which already exists for other bodies in our solar system and far beyond. The scientific and societal imperatives are clear—and the clock is ticking.

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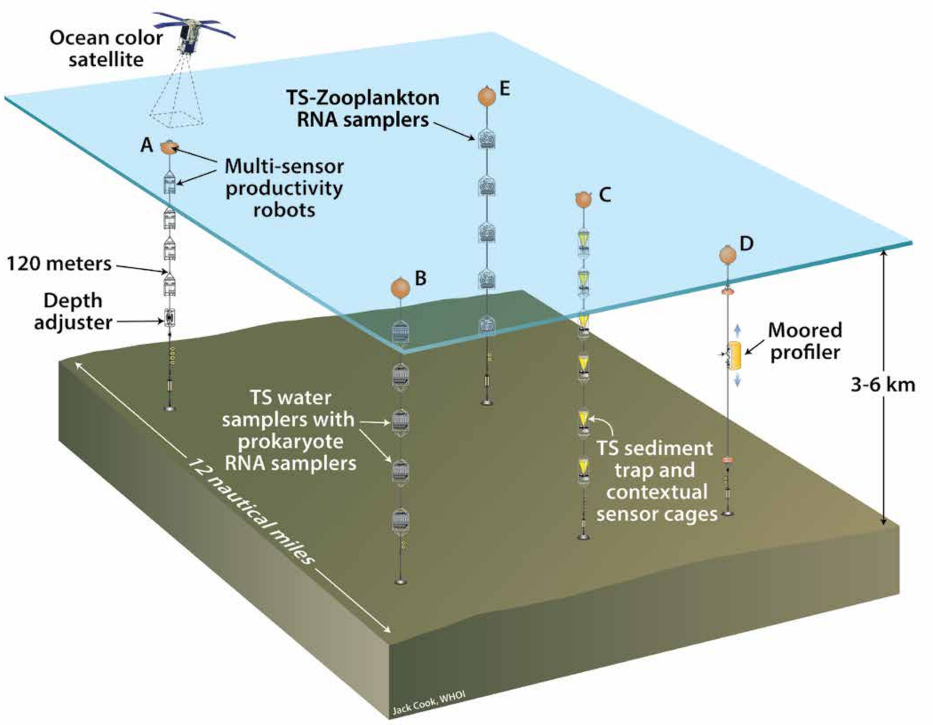

Figure 3. A preliminary vision of a Global Biogeochemical Flux Observatory (GBF-O) instrumented mooring array for sustained deployment at a given ocean location. The array consists of five moorings that include (A) primary production measurements, (B) in situ time-series (TS) water samplers and quantitative prokaryote collectors that preserve RNA, (C) TS sediment traps to capture settling POC and other particulate matter, (D) a moored profiler for seamless recording of conductivity-temperature-depth, current, and acoustic ecosystem imaging data, and (E) quantitative zooplankton samplers with autonomous RNA fixing processors. Further details are in the Online Supplement, Section 4.

ONLINE SUPPLEMENT

The Online Supplement can be accessed at http://www.tos.org/oceanography/archive/27-3_honjo.html.

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