Biological Pump

Sarah L. C. Giering[1] and Matthew P. Humphreys[2]
[1]Ocean Biogeochemistry and Ecosystems, National Oceanography Centre, Southampton, UK
[2]Ocean and Earth Science, University of Southampton, Southampton, UK

Definition

The biological pump is the collection of marine biogeochemical processes that convert dissolved inorganic matter in the surface ocean into biomass and transport this to the ocean interior, where the biomass is returned to its original dissolved inorganic forms.

Introduction

The concentrations of elements vary throughout the global ocean. Concentrations of dissolved inorganic carbon (DIC – the sum of the aqueous CO_2 (<1%), bicarbonate (~90%), and carbonate ion (~10%) concentrations) and nutrients are greater in deep waters relative to the near-surface, and in older water masses relative to younger ones. Some trace metals, on the other hand, have higher concentrations in surface waters. The biological pump is an important process that contributes to these gradients.

The biological pump begins in the sunlit upper ocean, called the euphotic zone. Here, photosynthesizing organisms convert DIC and nutrients into biomass, in the form of particular organic matter (e.g., carbohydrates, lipids, and proteins) and biominerals (e.g., calcium carbonate and silica). This biomass is constantly reworked in a complex web of trophic interactions, and is mostly converted back into an inorganic form within the surface ocean. However, a fraction of the organic matter is "exported" from the surface ocean into the deeper interior. There, these particles may dissolve or be processed by the resident biota, ultimately converting them back into their inorganic forms ("remineralization"). Most remineralization occurs in the upper 1000 m of the water column, although a fraction of the organic matter also reaches the deeper waters and seafloor sediments.

Export

"Export flux" is the rate per unit area at which biomass exits the surface ocean through a reference depth. A fixed reference depth of 100 m is often used for studies that are based on modeling or remote sensing. A dynamic reference depth, such as the base of either the mixed layer or the euphotic zone, is more appropriate to capture particle dynamics and compare export across different ecosystems (Buesseler and Boyd 2009). The ratio of export flux to primary production is called "export efficiency." Three processes can drive export from the surface layer: sinking, active transport, and physical transport.

Sinking

The euphotic zone overlaps with the surface mixed layer, which is physically separated from the interior ocean by a density gradient sustained by winds and air-sea heat and

freshwater fluxes. Nevertheless, a fraction of the organic matter passes through this density gradient in the form of sinking particles or through active transport. Sinking particles are a major pathway for biomass transfer to depth. These particles range in diameter from a few micrometers to several centimeters, and particles >0.5 mm across are called "marine snow." Each particle's sinking speed is determined by its density and drag, with larger particles generally sinking faster. The incorporation of biominerals, such as biogenic silica produced by diatoms, increases density and can thus increase the sinking speed. Large particles are produced primarily through aggregation, which occurs through "coagulation" or biologically mediated repackaging (Burd and Jackson 2009). Coagulation requires particles to stick together to form a larger particle. "Stickiness" is currently not well understood but may be mediated by cell shape (e.g., whether plankton cells have spines or form chains) and the presence of exopolymers (e.g., transparent exopolymer particles) (Burd and Jackson 2009). Aggregation can further occur through feeding and repackaging by larger zooplankton and fish, which results in growth (i.e., biomass accumulation) and the production of fecal pellets (Steinberg and Landry 2017). The sinking of carcasses, in particular those of jellyfish and mammals, could be a significant contributor to export, but remains poorly quantified.

Active Transport

Larger zooplankton and fish export organic matter through vertical migration (Steinberg and Landry 2017). Many larger zooplankton feed in the mixed layer at night and retreat to a depth of several hundred meters during the day, in a process called "diel vertical migration." While resting at depth, migrating animals continue to respire, excrete, and release fecal material, and may die. Migrating animals thus actively export organic matter. The fraction of total export driven by diel vertical migration could be up to 40% (Brierley 2014). On seasonal timescales, some zooplankton species transport organic matter deeper still as they overwinter at over 1 km depth (Steinberg and Landry 2017). There is an additional nondiurnal contribution to active transport by krill, fish, and marine mammals.

Physical Transport

Physical transport can occur in areas of deep water formation, such as in the subpolar North Atlantic and the Southern Ocean. There, cold air takes up heat from warm, poleward-flowing surface waters, thus increasing their density and allowing them to sink to depths of up to 4 km. In the subtropical gyres, wind-driven downwelling can subduct surface waters into the interior (Carlson et al. 2010; Fontela et al. 2016). On smaller spatial scales, export via "detrainment" (i.e., the "mixed layer pump") can occur where stratification is unstable. A prominent example occurs during the onset of spring stratification at high latitudes (Dall'Olmo and Mork 2014). Rising air temperatures allow weak stratification to develop, promoting surface layer carbon fixation through phytoplankton production. During this time, unstable weather conditions (e.g., strong winds) can induce short-term mixed layer deepening, thus mixing the new biomass to greater depth. Once stratification strengthens again, this biomass remains isolated from the surface ocean. Export through detrainment has occurred if the biomass is not mixed back to the surface (or "entrained") during subsequent mixing events. These different types of vertical water mass transport can carry nonsinking organic matter and biominerals into the deep ocean.

Remineralization and Transfer

Most exported biomass is converted back into a dissolved inorganic form in the interior ocean through a set of processes together called remineralization. The remineralization rate, coupled with the vertical and horizontal transport, thus influences the distribution of dissolved inorganic matter, as well as its residence time in the interior ocean.

Sinking is the most effective export process for transporting biomass beyond a few hundred meters' depth, as active and physical transport are often restricted to the upper water column. Sinking particles can also penetrate density gradients and thus travel through different water masses, potentially reaching the seafloor. The "transfer efficiency" quantifies the fraction of organic matter exported from the surface layer that subsequently reaches a deeper reference depth (typically chosen between 500 and 2000 m).

Vertical Profiles

For sinking particles, transfer efficiency is a function of sinking speed and remineralization rate: fast remineralization and slow sinking retains matter near the surface ocean, while slow remineralization and fast sinking allow organic matter to be transported much deeper. Assuming that remineralization rate (r) and sinking speed (v) are constant with depth, flux (F_z) at a depth (z) can be calculated from a reference flux (F_{z0}) as:

(1) $F_z = F_{z0}\, e^{-(rz)/v}$

Observations of particle flux profiles suggest that particle flux is better described by an empirical power-law function known as the "Martin curve" (Martin et al. 1987):

(2) $F_z = F_{z0}\, (z\,/\,z_0)^{-b}$

This power-law function implies that particle sinking speeds increase, and/or remineralization rates decrease, with depth. For carbon, "Martin's coefficient" b varies regionally with a global average of 0.86, while other elements have different values due to varying remineralization and transfer rates (Boyd et al. 2017).
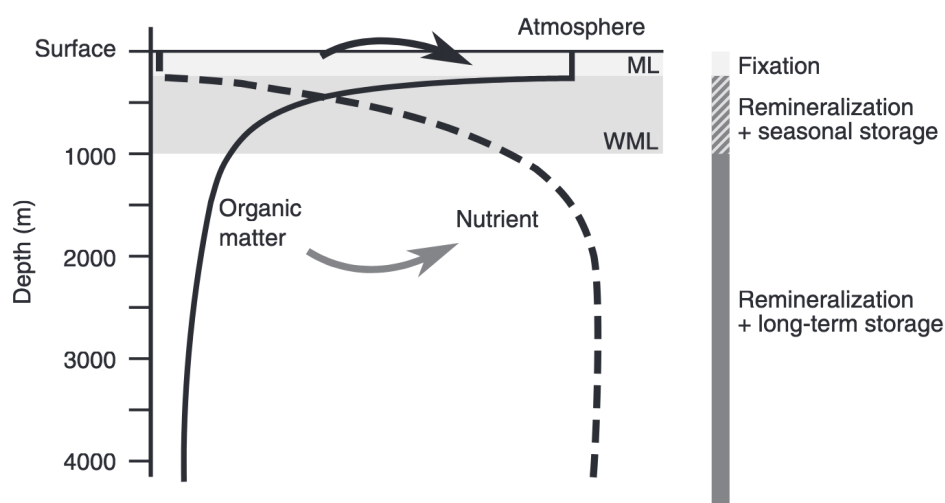

Figure 1. Idealized depth profiles of organic matter (solid line) and inorganic nutrients (dashed line). Mixed layer (ML) and winter mixed layer (WML) are illustrated by the green and blue areas, respectively. "Long-term" refers to time scales of up to about 1000 years. Arrows indicate fixation (black) and remineralization (gray).

As particles sink, they undergo transformation: remineralization and dissolution returns biomass into its dissolved components, while adsorption onto sinking particles removes dissolved elements from the water and transports these to the sediments. The unique combination of chemical and biological processes affecting each element thus drives its distinct vertical profile.

Depletion of an element in the surface layer indicates biological uptake, and such elements can limit primary production (they are "bio-limiting"). These elements are rapidly remineralized near the surface ocean, leading to increased concentrations of their dissolved form at depth ("nutrient-type profile"; Figure 1). Prominent examples are N, P, Si, Fe, Cd, and Zn (Johnson et al. 2017). Elements that follow the nutrient-type profiles but only show slight surface depletion are called "bio-intermediates," such as Sr which is only used by relatively rare planktonic organisms. Other bio-intermediate examples are C, Ba and Ca.

The adsorption of ions onto sinking particles removes dissolved elements from the water column. This process is more pronounced in surface waters, where particle concentrations are high, and in older, deeper water masses. Adsorption results in decreasing concentrations with depth ("scavenged profile"), with examples being Pb, Mn, Sn, and Co. Short residence times of reactive elements (less than the ocean mixing time) further means that their source of origin influences their distribution, leading to unique depth profiles. Elements whose residence time is longer than the ocean mixing time show nearly uniform concentrations throughout the ocean and have a "conservative profile." Examples are Na, Mg, and Ca (Johnson et al. 2017).

Remineralization

Remineralization occurs via metabolic processes and dissolution. Exported organic matter provides the main energy source for organisms living beneath the sunlit surface. While microbes are principally responsible for remineralization, much of the rapid decrease in organic matter fluxes in the region just below the surface ocean (Figure 1) is attributed to zooplankton (Giering et al. 2014). Zooplankton fragment large, fast-sinking particles into slow-sinking or suspended particles, thus facilitating shallow microbial remineralization. The metabolic requirements of microbes and zooplankton therefore determine the rate and processes responsible for remineralization.

Metabolic requirements vary for different elements, driving vertical decoupling. Compounds and elements that are essential to life are preferentially metabolized, so the majority of these are remineralized near the ocean surface. Remineralization is thus faster for macronutrients than for metals and approximately follows N > organic C > P > metals (Boyd et al. 2017).

Fresh aggregates are characterized by a high amount of labile compounds, such as essential amino acids and polyunsaturated fatty acids. Deep-sea organisms preferentially metabolize these labile compounds. Therefore, as organic matter "ages" (i.e., is processed), its lability decreases, and the contribution of saturated fatty acids and heterotrophic biomarkers increases (Lee et al. 2004). Eventually, the complex compounds are degraded into their inorganic forms and released as metabolic waste products. Organic nitrogen is converted to ammonia and then to nitrate by nitrifying bacteria. Organic phosphorus is excreted as phosphate. Organic carbon undergoes extensive reworking but is eventually respired as DIC.

Biominerals such as calcium carbonate and biogenic silica are produced along with organic matter. As they have little metabolic value to the deep-sea biota, their remineralization is determined by abiotic dissolution. The silica cycle illustrates how the biological pump influences elemental distributions in the ocean. The appearance of diatoms, which have high silicon requirements, led to a drop in silicic acid concentrations from ~1 mM to today's concentrations of ~70 uM, and resulted in a nutrient-type distribution for the past 50–100 million years (De La Rocha 2007).
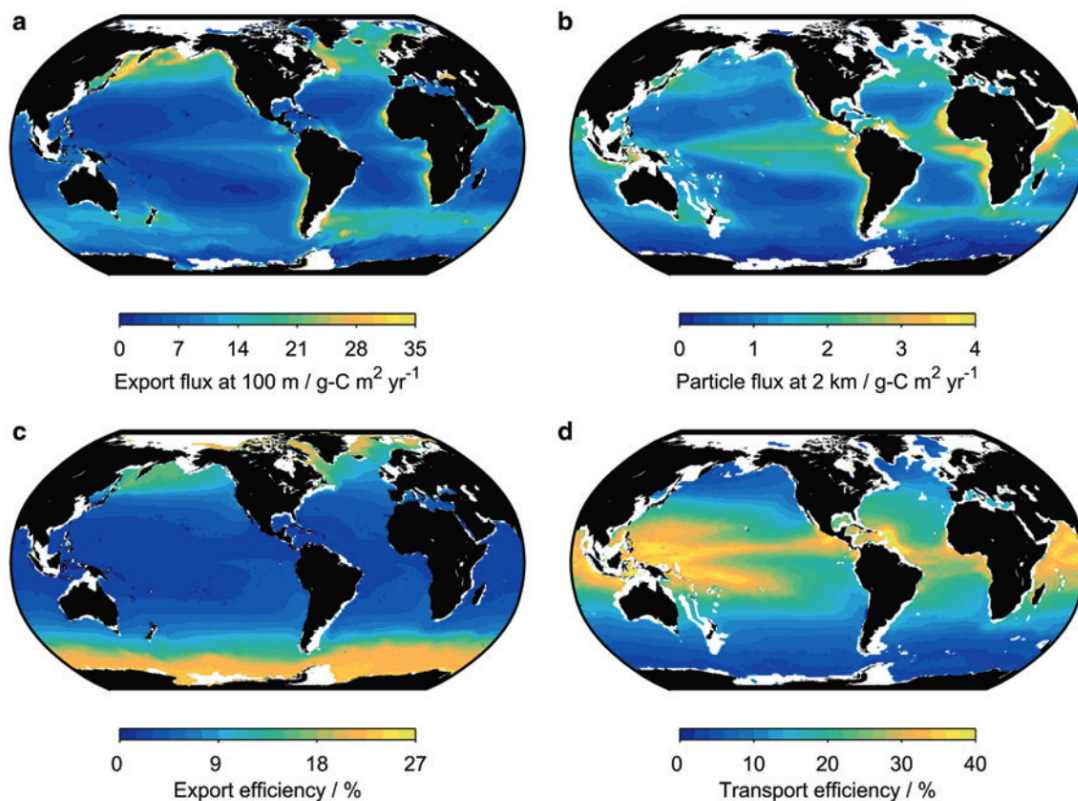

Figure 2. Global map of satellite-derived estimates of (a) export flux at 100 m depth, (b) particle flux at 2000 m depth, (c) export efficiency (flux at 100 m depth/depth-integrated primary production), and (d) transfer efficiency (flux at 2000 m/flux at 100 m). Redrawn from Henson et al. (2012). These maps show the approximate global patterns of each variable, but uncertainties for exact values at any specific location are high.

Biological Carbon Pump

The biological carbon pump transports 5–20 Gt carbon annually from the surface into the interior ocean (Henson et al. 2011), and keeps, according to models, the atmospheric CO_2 concentration much lower than without ocean biology (Parekh et al. 2006). However, its effect on surface layer CO_2 uptake differs depending upon the type of particulate material produced in the surface ocean.

The soft-tissue pump converts DIC into organic matter in the surface layer. This acts as a sink for atmospheric CO_2: More CO_2 can be added to the water, through air-sea exchange, to replace the DIC that was converted into organic matter. The carbonate "counter" pump converts DIC into particulate inorganic carbon (i.e., $CaCO_3$) through

near-surface calcification. Although this process also takes up DIC from the seawater, it reduces the total alkalinity of seawater (Wolf-Gladrow et al. 2007). Alkalinity controls the capacity for seawater to store DIC. The loss of alkalinity during calcification results in a reduction of the DIC storage capacity that is greater than the uptake of DIC. The net effect of calcification is therefore to drive the sea surface towards being a source of CO_2 to the atmosphere.

In the context of the biological carbon pump, the appropriate reference depth for export is the base of the winter mixed layer, because of the effect on isolation time from the atmosphere. DIC produced through remineralization above this depth will be mixed back up to the surface during the winter, where it is back in contact with the atmosphere, and thus promotes CO_2 outgassing. DIC produced beneath the winter mixed layer is considered to be isolated from the atmosphere until upwelling brings it back to the surface. The final isolation time depends on the location of particle export and depth of remineralization, and can be on the order of whole-ocean mixing (i.e., about 1000 years).

Global Pattern

While there is still much uncertainty about the absolute magnitude of export, remineralization, and transfer, general global patterns have been identified (Henson et al. 2012; Siegel et al. 2014). Export flux is typically higher at high latitudes, in the equatorial Pacific, and in upwelling regions (Figure 2a). Where primary production is strongly seasonal, export flux peaks during and after the phytoplankton bloom and is lowest during winter (Siegel et al. 2014). High-latitude regions can have high export efficiencies (Figure 2c), while low-latitude systems generally retain a large fraction of the organic matter in the surface ocean. Inversely, transport efficiency has been shown to increase towards the tropics (Figure 2d), leading to highest annual deep particle fluxes near the equator (Figure 2b) (Henson et al. 2012).

Climate and Bioengineering

Various "geo-engineering" techniques have been proposed to offset the impacts of the anthropogenic increase in atmospheric CO_2. Some aim to increase the ocean's capacity to take up and store carbon by enhancing the biological carbon pump. For example, iron addition could promote carbon fixation in areas where iron limits primary production, like the Southern Ocean. Experiments have confirmed that this approach can boost primary production, thus enhancing CO_2 uptake (Lampitt et al. 2008). However, for long-term CO_2 storage, the newly produced organic carbon must be transported below the winter mixed layer. An artificially fertilized, diatom-dominated bloom in the Southern Ocean exported more than half of its biomass to deeper than 1000 m, providing successful long-term DIC storage (Smetacek et al. 2012). However, little carbon was exported to the ocean interior in a similar experiment in the Subantarctic Atlantic Ocean, despite a short-term increase in primary production near the surface (Martin et al. 2013). This spatial variability in efficiency, coupled with concerns about disruptive effects on ecosystems, has led to skepticism that this technique could mitigate the adverse effects of anthropogenic CO_2 (Strong et al. 2009).

Summary

Through the biological pump, dissolved inorganic matter is converted into biomass in the surface ocean, and exported to the interior via sinking, active transport or physical transport. At depth, this biomass is processed (fragmented and/or repackaged) by deep-sea organisms and remineralized. Essential elements are remineralized near the surface ocean and thus have "nutrient-type" vertical profiles (increasing concentration with depth). Non-essential elements exhibit a variety of profiles including decreasing concentrations with depth ("scavenged") and uniform distributions ("conservative"). The storage of carbon in the interior ocean sustained by the biological carbon pump plays an important role in regulating the atmospheric CO_2 concentration. The biological pump thus sustains life in the deep sea and drives the spatial distributions of many elements throughout the global ocean.

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