



Review

Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump



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ABSTRACT

The “biological pump” is the process by which photosynthetically-produced organic matter in the ocean descends from the surface layer to depth by a combination of sinking particles, advection or vertical mixing of dissolved organic matter, and transport by animals. Particulate organic matter that is exported downward from the euphotic zone is composed of combinations of fecal pellets from zooplankton and fish, organic aggregates known as “marine snow” and phytodetritus from sinking phytoplankton. Previous reviews by Turner and Ferrante (1979) and Turner (2002) focused on publications that appeared through late 2001. Since that time, studies of the biological pump have continued, and there have been >300 papers on vertical export flux using sediment traps, large-volume filtration systems and other techniques from throughout the global ocean. This review will focus primarily on recent studies that have appeared since 2001. Major topics covered in this review are (1) an overview of the biological pump, and its efficiency and variability, and the role of dissolved organic carbon in the biological pump; (2) zooplankton fecal pellets, including the contribution of zooplankton fecal pellets to export flux, epipelagic retention of zooplankton fecal pellets due to zooplankton activities, zooplankton vertical migration and fecal pellet repackaging, microbial ecology of fecal pellets, sinking velocities of fecal pellets and aggregates, ballasting of sinking particles by mineral contents, phytoplankton cysts, intact cells and harmful algae toxins in fecal pellets, importance of fecal pellets from various types of zooplankton, and the role of zooplankton fecal pellets in picoplankton export; (3) marine snow, including the origins, abundance, and distributions of marine snow, particles and organisms associated with marine snow, consumption and fragmentation of marine snow by animals, pathogens associated with marine snow; (4) phytodetritus, including pulsed export of phytodetritus, phytodetritus from *Phaeocystis* spp., picoplankton in phytodetritus, the summer export pulse (SEP) of phytodetritus in the subtropical North Pacific, benthic community responses to phytodetritus; (5) other components of the biological pump, including fish fecal pellets and fish-mediated export, sinking carcasses of animals and macrophytes, feces from marine mammals, transparent exopolymer particles (TEP); (6) the biological pump and climate, including origins of the biological pump, the biological pump and glacial/interglacial cycles, the biological pump and contemporary climate variations, and the biological pump and anthropogenic climate change. The review concludes with potential future modifications in the biological pump due to climate change.

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Introduction

The ocean's biological pump

The “biological pump” is the process through which photosynthetically-produced organic matter in the ocean is exported from the surface layer to depth by a combination of sinking particles, advection or vertical mixing of dissolved organic matter, and transport by animals.

Together with the “solubility pump” (Volk and Hoffert, 1985), whereby the solubility of CO₂ increases with depth due to colder water at depth, the biological pump (Fig. 1) is a major part of the process that draws down carbon from the atmosphere into the surface layers of the ocean, where carbon is dissolved in seawater, converted to particulate form through primary production, then consumed by pelagic biota, exported to depth, and/or sequestered in the deep sea (Volk and Hoffert, 1985; Longhurst and Harrison, 1989; Longhurst, 1991; Ducklow et al., 2001). It is estimated that the biological pump annually removes >10 billion tons of carbon from the ocean's epipelagic waters (Buesseler and Boyd, 2009), but only about 10% of that flux reaches the bottom of the mesopelagic zone (Martin et al., 1987). Passow and Carlson (2012) suggested that approximately two-thirds of the vertical gradient in carbon in the sea is due to the biological pump, with the remainder due to the solubility pump.

The biological pump is relatively inefficient. Most of the carbon fixed into phytoplankton cells through near-surface photosynthesis is remineralized in the epipelagic zone (upper 100–200 m) or upper layers of the mesopelagic zone (100–200 to 1000 m). Generally, only about 5–25% of net primary production is exported from the euphotic zone (De La Rocha and Passow, 2007, and references therein), but export varies with location. Export of net primary production from the euphotic zone is usually <10% (Neuer et al., 2002b) in central gyres but may be as much as 30–100% in

polar waters (Buesseler, 1998). Usually only <3% of net primary production reaches bathypelagic depths (>1000 m) in the deep sea (De La Rocha and Passow, 2007, and references therein). Such variability in export to depth is partly due to variability in the planktonic food webs in overlying epipelagic waters (Legendre and Rivkin, 2002). The >97% of net primary production that does not reach the deep sea is consumed or respired in the water column, with approximately 15% being processed by bacteria (Ducklow, 2000), 30–70% by microzooplankton 20–200 µm in size (Calbet and Landry, 2004) and 20–35% by the >200 µm mesozooplankton (Hernández-León and Ikeda, 2005).

Passow and Carlson (2012) distinguished the “export flux” leaving the bottom of the euphotic zone (at approximately 100 m depth) from the “sequestration flux” from the bottom of the mesopelagic zone (at approximately 1000 m depth), because once carbon is transported below the sequestration depth, it remains in the deep sea longer than 100 years. Passow and Carlson (2012) noted that the export flux from the base of the euphotic zone approximately equals new photosynthetic production based on new nitrogen, such as nitrate input to the euphotic zone due to convective mixing or upwelling from below, plus allochthonous sources such as atmospheric deposition, horizontal advection or nitrogen fixation. However, sequestration flux appears to be primarily dependent on flux attenuation and remineralization of organic matter in the mesopelagic zone (Passow and Carlson, 2012). Rather than using a single depth for sequestration depth, Antia et al. (2001) used the depth of winter mixing for sequestration depth for various locations in the Atlantic. Sequestration depth varied with location, due to differences in the depth of winter mixing. Euphotic zone depth also varies with location, so Antia et al. (2001) concluded that export depth and sequestration depth were better defined by light penetration and mixing rather than by fixed depths.

Inefficient but rapid export by the biological pump has been independently confirmed by serendipitous “tracer experiments”

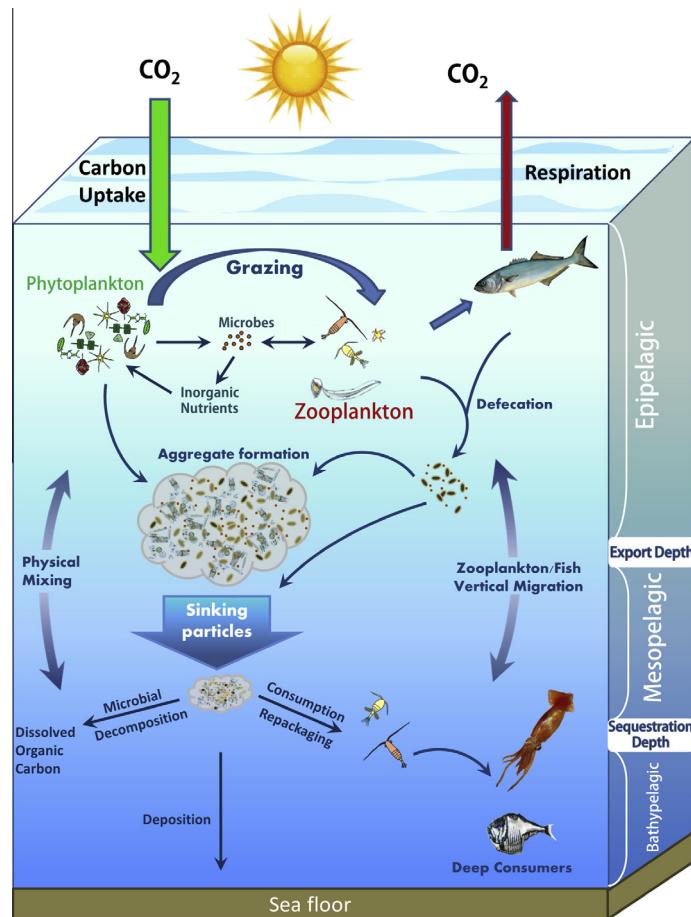


Fig. 1. The biological pump in the ocean. CO_2 is drawn into the ocean from the atmosphere, and dissolved CO_2 is processed into particulate organic carbon (POC) through photosynthesis by the phytoplankton in the euphotic layer of the epipelagic zone (0–200 m depth). Organic matter in epipelagic phytoplankton is processed by microbes, zooplankton, and their consumers into fecal pellets, organic aggregates (“marine snow”), and other forms of POC, which are exported to the mesopelagic and bathypelagic zones by sinking and vertical migration by zooplankton and fish. The export depth is sometimes identified as the bottom of the euphotic zone, or as the maximum mixed layer depth, both of which are variable, but usually lie at approximately 100 m depth. Dissolved organic carbon (DOC) is produced by microbial remineralization, and can be mixed either upward or downward through physical vertical mixing of water. In the mesopelagic zone (200–1000 m depth), microbial decomposition and zooplankton/fish consumption and repackaging of POC and DOC continue, with dramatic attenuation of export flux as organic compounds are remineralized into inorganic nutrients and other compounds. The sequestration depth is the depth below which carbon is stored in the ocean for 100 years or more. The sequestration depth has sometimes been designated as the bottom of the mesopelagic zone (Passow and Carlson, 2012), but in other treatments as the maximum depth of winter mixing, which in the Atlantic can be between 100 and 800 m (Antia et al., 2001).

using collections of radionuclides from nuclear power plant accidents in deep-sea sediment traps. Honda et al. (2013) found that sediment traps already in place in the northwestern Pacific prior to the accident at the Fukushima Daiichi Nuclear Power Plant (11 March 2011) collected radionuclides (^{134}Cs and ^{137}Cs) from the accident in a few weeks at 500 m, and in approximately a month at 4810 m. However, estimated removal rates for ^{137}Cs were only $0.3\text{--}1.5\% \text{ yr}^{-1}$. These removal rates were comparable to those of 0.2–1% recorded for several radionuclides from the Chernobyl nuclear power plant accident (26 April 1986) collected in sediment traps within days at 200 m in the northern Mediterranean (Fowler et al., 1987) and at 222 m in the North Sea (Kempe and Nies, 1987; Kempe et al., 1987), several months afterward in sediment traps at 1071 m in the Black Sea (Buesseler et al., 1987; Kempe et al., 1987), or at depths of 110–780 m the North Pacific and Bering Sea (Kusakabe et al., 1988). Although Fukushima-derived radionuclides were collected in zooplankton and mesopelagic fish (Buesseler et al., 2012), indicating export by the biological pump, radionuclide concentrations were extremely low. However, due to their long residence times, Fukushima-derived radionuclides will be useful as tracers for water mass transport in the northwest Pacific Ocean for decades (Povinec et al., 2013).

Variability in the efficiency of the ocean’s biological pump is sensitive to climate. The biological pump is hypothesized to have contributed to fluctuations in levels of atmospheric carbon dioxide during past glacial–interglacial periods (Sigman and Boyle, 2000; Kohfeld et al., 2005). The biological pump also responds to contemporary variations in climate (Dunne et al., 2007; Lutz et al., 2007; Smith Jr. et al., 2009; Lomas et al., 2010; Wilson et al., 2013). How the ocean’s biological pump will respond to future anthropogenic climate change is uncertain (Bopp et al., 2001; Heinze, 2004; Sarmiento et al., 2004; Oschlies et al., 2008; Hofmann and Schellnhuber, 2009; Reid et al., 2009; Riebesell et al., 2009; Wohlers et al., 2009; Passow and Carlson, 2012, and references therein).

It has long been thought that zooplankton fecal pellets are an important component of the biological pump in the sea. Turner and Ferrante (1979) reviewed literature on importance of zooplankton fecal pellets in marine and freshwater ecosystems. Included were considerations of the vertical particulate transport potential, nutritional content, recycling by decomposition and coprophagy (ingestion of fecal pellets), and pollutant content of zooplankton fecal pellets.

The review of Turner and Ferrante (1979) was updated by Turner (2002). The intervening two decades between these two reviews saw >500 publications from studies in marine waters with

sediment traps, particle interceptor traps and large-volume filtration systems that had appeared since the review of [Turner and Ferrante \(1979\)](#). These studies revealed that while sinking zooplankton fecal pellets generally remain important in the vertical flux of particles and chemicals from the near-surface to deeper layers of the sea, in many cases zooplankton fecal pellets are recycled and thereby “retained” in the upper few hundred meters of the water column by coprophagy and microbial decomposition. Further, in many cases much, if not most, of the vertical flux is not due to fecal pellets, but to marine snow, and sedimenting phytoplankton blooms that sink to the benthos without contributing appreciably to pelagic food webs.

[Turner \(2002\)](#) cited most papers on zooplankton fecal pellets, marine snow and sinking phytoplankton blooms that had been published from 1979 through late 2001. Since that time, however, studies of the biological pump have continued. Thus, the present review focuses mainly on papers that have appeared since 2001, including papers that were published in 2001 but were not cited in the [Turner \(2002\)](#) review, as well as papers that have been published from 2002 through mid-2014.

Results from >300 studies since 2001 of vertical export flux using sediment traps, large-volume filtration systems and other techniques from all over the global ocean ([Table 1](#)) exhibit several generalities, noted below. Vertical flux of sinking particles is usually due to a combination of fecal pellets, marine snow and direct sedimentation of phytoplankton blooms ([De La Rocha and Passow, 2007](#); [Buesseler et al., 2008b](#)). Aggregation of particles enhances vertical flux by transforming small suspended particles into larger rapidly-sinking ones. Aggregation is important in the sedimentation of phytodetritus from surface layer phytoplankton blooms. Sedimenting phytoplankton blooms are typically composed mainly of diatoms, coccolithophorids, gelatinous colonial species of the genus *Phaeocystis*, dinoflagellates, and other plankton ([Beaulieu, 2002](#)). The relative contributions of fecal pellets, marine snow and phytodetritus to total particulate flux vary considerably in time and space, and with the abundances and composition of the phytoplankton, zooplankton, and microbial plankton communities in epipelagic waters ([Gleiber et al., 2012](#); [Wilson et al., 2013](#)). “Retention” of fecal pellet components in near-surface waters, rather than export of fecal pellet components to abyssal depths, is due to combinations of microbial degradation and zooplankton-mediated processes such as disruption of fecal pellets by zooplankters ([Svensen et al., 2012](#)). As noted by [Buesseler and Boyd \(2009\)](#), “the surface ocean” is “where the ‘strength’ of the biological pump is set” whereas “the subsurface ocean” is “where the ‘efficiency’ of the biological pump is determined.” Simulations by [Legendre and Rivkin \(2002\)](#) suggest that the phytoplankton community controls the export of phytodetritus, the microbial food web controls most remineralization of organic carbon to carbon dioxide, and large zooplankton are responsible for most transfer of particulate organic carbon to large metazoans, through fecal pellets and vertically-migrating animals.

Recent studies of the export flux of particulate organic carbon (POC)

The downward export of POC by the biological pump has variable efficiency due to the abundance and composition of near-surface plankton communities, and recycling and attenuation of the flux of sinking particles at depth.

There have been hundreds of publications on the concentrations and/or vertical export flux of particulate organic materials that have been published since 2001 ([Table 1](#)). Most of these measurements have been done using sediment traps, which due to differences in design and/or details of deployment, can give highly-variable and sometimes incomparable results ([Buesseler et al., 2007a](#)). There have also been several extensive reviews of the

export flux of organic particulates ([Boyd and Trull, 2007](#); [Buesseler and Boyd, 2009](#); [Buesseler et al., 2007b](#); [De La Rocha and Passow, 2007](#); [François et al., 2002](#); [Honjo et al., 2008](#)). Other reviews related to various aspects of the biological pump include those of [Arístegui et al. \(2009\)](#), [Beaulieu \(2002\)](#), [Bishop \(2009\)](#), [Boyd and Stevens \(2002\)](#), [Burd and Jackson \(2009\)](#), [Burd et al. \(2010\)](#), [Frangoulis et al. \(2005\)](#), [Kiørboe \(2001\)](#), [Koeve \(2005, 2006\)](#), [MacGilchrist et al. \(2014\)](#), [Passow \(2002a, 2002b\)](#), [Sanders et al. \(2014\)](#), [Simon et al. \(2002\)](#), and [Stemann and Boss \(2012\)](#).

There is considerable variability in the export flux of POC. This variability can be seasonal (examples include [Conte et al., 2001](#); [Ducklow et al., 2008](#); [Gleiber et al., 2012](#); [Lampitt et al., 2001, 2010](#); [Lutz et al., 2007](#); [Michel et al., 2002](#); [Miquel et al., 2011](#); [Smith Jr. et al., 2006a, 2006b](#); [Takahashi et al., 2002](#)) and/or inter-annual (examples include [Conte et al., 2001](#); [Ducklow et al., 2006](#); [Fortier et al., 2002](#); [Gleiber et al., 2012](#); [Heimbürger et al., 2013](#); [Kim et al., 2012](#); [Lampitt et al., 2010](#); [Lomas et al., 2010](#); [Miquel et al., 2011](#); [Smith Jr. et al., 2011b](#); [Steinberg et al., 2012](#); [Waniek et al., 2005](#)). There is also variability in export fluxes due to climatological variations such as El Niño–Southern Oscillation ([Boyd and Trull, 2007](#); [Kim et al., 2014](#); [Shipe et al., 2002](#)), Indian Ocean monsoon ([Rixen et al., 2005](#)), North Atlantic Oscillation ([Lomas et al., 2010](#)), and North Pacific Gyre Oscillation ([Sekula-Wood et al., 2011](#)) cycles.

Much of the variability in the export flux to depth is related to the abundance and composition of the overlying plankton community ([Atkinson et al., 2012](#); [Ducklow et al., 2006](#); [Gleiber et al., 2012](#); [Guidi et al., 2009](#); [Henson et al., 2012a](#); [Lalande et al., 2011](#); [Lomas et al., 2010](#)). [Guidi et al. \(2009\)](#) performed a global ocean synthesis of vertical profiles and size distributions of large (>1 mm) particles down to 1 km depth in relation to phytoplankton size distributions in surface waters. Where there were larger particles in the mesopelagic layer, there was mainly microplankton (>20 µm) in the euphotic zone, but where there were mainly smaller particles in the mesopelagic zone, there was mainly picoplankton (<2 µm) in the euphotic zone.

There have been long-term increases in zooplankton biomass in the subtropical gyres of both the North Atlantic ([Steinberg et al., 2012](#)) and North Pacific ([Sheridan and Landry, 2004](#)). These increases in zooplankton have been associated with increases in amounts of both active carbon flux through zooplankton vertical migration and sinking flux of zooplankton fecal pellets ([Steinberg et al., 2012](#)), as well as increased migrant flux of phosphorus from surface waters to depth ([Hannides et al., 2009](#)).

The transfer efficiency of sinking POC between 150 and 500 m differed at two stations in the North Pacific ([Boyd et al., 2008](#); [Buesseler et al., 2007b](#); [Lamborg et al., 2008](#)). At Station ALOHA (A Long-term Oligotrophic Habitat Assessment) in the oligotrophic subtropical gyre in the Hawaii Ocean Time-series (HOT) study, there were consistently low nutrients and warm temperatures near-surface, resulting in a picoplankton-dominated system with low seasonality, low primary production and low POC flux to the base of the euphotic zone. At Station K2 in the northwest Pacific subarctic gyre, there were colder high-nutrient waters, the phytoplankton was dominated by diatoms, with higher phytoplankton biomass, productivity and vertical export. Flux attenuation, measured by mesopelagic transfer efficiency (the ratio of POC flux at 500–150 m) was only 20% at ALOHA, but was 46–55% at K2. Most of the identifiable exported particulates at K2 were zooplankton fecal pellets from larger copepods, which presumably sank faster than the smaller fecal pellets found at ALOHA. [Buesseler et al. \(2007b\)](#) concluded that the higher transfer efficiency to depth at K2 was also due to particulates containing abundant diatom cells with higher mineral ballasting by biogenic silica, than for the non-mineralized picoplankton and particulate inorganic carbonate-containing coccolithophorids at ALOHA. Thus the differences

Table 1

Studies of concentrations and/or vertical export flux of particulate organic materials using sediment traps, *in situ*- pumping systems, discrete water samples, and other techniques, that were either published in 2001 but not cited in Turner (2002), or that have been published since 2002.

Arctic/subarctic

- Central Arctic Ocean – Olli et al. (2007)
- Barents Sea – Coppola et al. (2002), Gustafsson and Andersson (2012), Olli et al. (2002), Reigstad et al. (2008, 2011), Tamelander (2013), Tamelander et al. (2006), Wassmann et al. (2006), (2008), Wexels Riser et al. (2002, 2007, 2008)
- Kara Sea – Gaye et al. (2007)
- Balsfjord, Norway – Reigstad and Wassmann (2007), Tamelander (2013), Wexels Riser et al. (2010)
- Northern Norwegian fjords – Belviso et al. (2006)
- Eurasian sector of the Central Arctic Ocean – Gustafsson and Andersson (2012)
- European Arctic Ocean – Tamelander et al. (2013)
- Fram Strait – Bauerfeind et al. (2009), Kraft et al. (2013), Lalande et al. (2011, 2013)
- Iceland Basin – Rynearson et al. (2013)
- Greenland Sea, Fram Strait, Barents Sea – Tamelander et al. (2012)
- Northeast Water Polynya – Pesant et al. (2002)
- Disko Bay, West Greenland – Dünweber et al. (2010), Juul-Pedersen et al. (2006)
- Sub-polar North Atlantic – Briggs et al. (2011), Martin et al. (2011)
- Labrador Sea – Moran et al. (2003)
- Newfoundland – Thompson et al. (2008)
- Canada Basin – Baskaran et al. (2003), Honjo et al. (2010), O'Brien et al. (2013)
- The North Water Polynya (northern Baffin Bay) – Acuña et al. (2002), Amiel et al. (2002), Booth et al. (2002), Caron et al. (2004), Deming et al. (2002), Hargrave et al. (2002), Michel et al. (2002), Sampei et al. (2002, 2004)
- Barrow Strait (Canadian Arctic Archipelago) – Fortier et al. (2002)
- Hudson Bay, Canada – Lalande and Fortier (2011), Lapoussière et al. (2009, 2013)
- Western Canadian Arctic – Juul-Pedersen et al. (2008)
- Central Arctic Ocean – Fahl and Nöthig (2007), Olli et al. (2007)
- Beaufort Sea – Forest et al. (2007, 2010), Juul-Pedersen et al. (2010), Sampei et al. (2009a, 2009b, 2012)
- Bering Strait Shelf – Cooper et al. (2009)
- Eastern Bering Sea – Baumann et al. (2013)
- Bering Sea and central subarctic Pacific Ocean – Takahashi et al. (2002)
- Chukchi Sea – Honjo et al. (2010), Lalande et al. (2007), Moran et al. (2005)
- Western Arctic Ocean – Lepore and Moran (2007)
- Northeast Subarctic Pacific Ocean – Boyd et al. (2005), Timothy et al. (2013)
- Western Subarctic Pacific – Aramaki et al. (2009), Boyd et al. (2008), Buesseler et al. (2007b, 2008b), Elskens et al. (2008), Kobari et al. (2003, 2008, 2013), Lamborg et al. (2008), Steinberg et al. (2008a, 2008b), Takahashi et al. (2009), Trull et al. (2008b), Tsuda et al. (2003), Wilson et al. (2008, 2010), Wilson and Steinberg (2010)
- Alaska Gyre – Tsurumi et al. (2005)

Antarctic

- South Indian Ocean – Coppola et al. (2005), Pasquer et al. (2010), Pilskaln et al. (2004)
- Kerguelen Plateau (Indian Ocean) – Blain et al. (2007), Ebersbach and Trull (2008), Jouandet et al. (2008, 2011), Savoye et al. (2008), Trull et al. (2008a)
- Crozet Islands (Indian Ocean) – Morris and Sanders (2011), Planquette et al. (2011), Pollard et al. (2009), Salter et al. (2012)
- Crozet Plateau (Indian Ocean) – Hernandez-Sanchez et al. (2012), Morris et al. (2007), Salter et al. (2007)
- Ellis Fjord (east Antarctica) – Beaumont et al. (2001, 2002)
- Atlantic sector – Friedrich and Rutgers van der Loeff (2002), Walter et al. (2001), Ebersbach et al. (2014)
- Lazarev Sea – Pakhomov et al. (2002)
- Polar Front Region (SE Atlantic) – Fischer et al. (2002), Rutgers van der Loeff et al. (2002)
- Eastern Weddell Sea shelf – Isla et al. (2006)
- Antarctic Circumpolar Current (Atlantic) and Weddell Sea – Rutgers van der Loeff et al. (2011), Veit-Köhler et al. (2011)
- Western Weddell Sea – Michels et al. (2008)
- Weddell Sea and Scotia Sea – Shaw et al. (2011), Sherman et al. (2011), Smith Jr. (2011), Smith Jr. et al. (2011)
- Deception Island – Baldwin and Smith (2003)
- Eastern Bransfield Strait – Kim et al. (2005)
- Western Bransfield Strait – Anadón and Estrada (2002), Anadón et al. (2002), Masqué et al. (2002), Palanques et al. (2002a, 2002b)
- West Antarctic Peninsula and Ross Sea – Ducklow et al. (2006)
- Western Antarctic Peninsula continental shelf – Buesseler et al. (2010), Daniels et al. (2006), Ducklow et al. (2008), Gleiber et al. (2012), McDonnell and Buesseler (2010), Sailley et al. (2013), Smith et al. (2008a), Walsh et al. (2001), Weston et al. (2013)
- Ross Sea – Asper and Smith (2003), Becquevert and Smith (2001), Smith Jr. et al. (2011)
- Terra Nova Bay – Manno et al. (2010)
- Subantarctic and Polar Front Zones south of Tasmania – Ebersbach et al. (2011), Jacquet et al. (2011)
- Pacific sector of the Southern Ocean (170°W) – Buesseler et al. (2001, 2003), Green and Sambrotto (2006), Ingalls et al. (2006a), Nelson et al. (2002)
- Pacific sector south of Australia – Bakker et al. (2006), Boyd and Law (2001), Boyd et al. (2002), Jackson et al. (2005), Nodder et al. (2001), Waite and Nodder (2001)
- Southern Ocean – Berelson (2001), Bishop et al. (2004), Buesseler (2012), Buesseler et al. (2004), Coale et al. (2004), Honjo (2004), Lam and Bishop (2007), Smetacek et al. (2012), Primeau (2006), Suzuki et al. (2003), Tesi et al. (2012), Yu et al. (2001)

Temperate

- Norwegian fjords, North Sea – Reigstad and Wassmann (2007)
- Aegean Sea – Frangoulis et al. (2010)
- NW Mediterranean – Andersen et al. (2009), Guidi et al. (2008), Jeffreys et al. (2011), Lopez-Fernandez et al. (2013a, 2013b), Martín et al. (2006), Marty et al. (2009), Miquel et al. (2011), Pagès et al. (2007), Rodriguez y Baena et al. (2007), Schmidt et al. (2002), Stemmann et al. (2002, 2004a, 2004b), Stewart et al. (2007)
- Ligurian Sea (NW Mediterranean) – Abramson et al. (2010), Armstrong et al. (2009), Cochran et al. (2009), Fowler et al. (2010), Heimbürger et al. (2013, 2014), Lee et al. (2009a, 2009b), Liu et al. (2009), Martin and Miquel (2010), Peterson et al. (2005, 2009), Szlosek et al. (2009), Tamburini et al. (2009), Verdeny et al. (2009), Wakeham et al. (2009), Xue and Armstrong (2009)
- Ligurian, Tyrrhenian, Aegean Seas – Speicher et al. (2006)
- Ionian Sea – Stavrakakis et al. (2013)
- Eastern Mediterranean – Koppelman et al. (2004)
- Krka estuary (eastern Adriatic) – Svensen et al. (2007)
- Bari canyon (Adriatic Sea) – Tesi et al. (2008)
- Mediterranean Sea and Long Island Sound – Liu et al. (2005)
- Mediterranean Sea and northwest Atlantic – Lepore et al. (2009)

(continued on next page)

- Algero-Balearic Basin (Western Mediterranean) – [Zuñiga et al. \(2007\)](#)
 Bay of Calvi (Western Mediterranean) – [Frangoulis et al. \(2011\)](#)
 Alboran Sea – [Masqué et al. \(2003\)](#)
 NW Africa – [Karakaş et al. \(2009\)](#), [Neuer et al. \(2002a\)](#)
 North Atlantic – [Abell et al. \(2013\)](#), [Alkire et al. \(2012\)](#), [Antia \(2005a, 2005b\)](#), [Berelson \(2001\)](#), [Carlson et al. \(2010\)](#), [Daniels et al. \(2006\)](#), [Guidi et al. \(2008\)](#), [Jackson and Checkley \(2011\)](#), [Primeau \(2006\)](#), [Usbeck et al. \(2003\)](#), [Yu et al. \(2001\)](#)
 NW Iberian Peninsula ria – [Varela et al. \(2004\)](#)
 Iberian shelf – [Álvarez-Salgado et al. \(2001\)](#), [Olli et al. \(2001a, 2001b\)](#), [Wexels Riser et al. \(2001\)](#)
 Nazaré submarine canyon (off Portugal) – [Martín et al. \(2011\)](#)
 Azores Triple Junction – [Khripounoff et al. \(2008\)](#)
 Canary Islands – [Abrantes et al. \(2002\)](#), [Alonso-González et al. \(2010\)](#), [Freudenthal et al. \(2001\)](#), [Pätsch et al. \(2002\)](#)
 Northeast Atlantic – [Fabiano et al. \(2001\)](#), [Giering et al. \(2014\)](#), [Guidi et al. \(2007\)](#), [Henson et al. \(2012a\)](#), [Jeffreys et al. \(2011\)](#), [Kiriakoulakis et al. \(2001, 2009\)](#), [Koeve et al. \(2002\)](#), [Lampitt et al. \(2001, 2008, 2009, 2010\)](#), [Le Moigne et al. \(2013\)](#), [Riley et al. \(2012\)](#), [Salter et al. \(2010\)](#), [Vanucci et al. \(2001\)](#), [Vilas et al. \(2009\)](#), [Waniek et al. \(2005\)](#), [Witbaard et al. \(2001\)](#)
 Baltic Sea – [Gustafsson et al. \(2006\)](#), [Tamelander and Heiskanen \(2004\)](#)
 Kattegat – [Lund-Hansen et al. \(2004\)](#)
 Gullmar Fjord, Sweden – [Gustafsson et al. \(2006\)](#), [Vargas et al. \(2002\)](#), [Waite et al. \(2005\)](#)
 North Sea – [Poulsen and Kiørboe \(2006\)](#), [Belviso et al. \(2006\)](#)
 Northwest Atlantic – [Hwang et al. \(2009, 2014\)](#)
 Gulf of St. Lawrence – [Romero-Ibarra and Silverberg \(2011\)](#)
 Cape Breton Island, Nova Scotia – [Hargrave et al. \(2007\)](#)
 Scotian Shelf – [Pommier et al. \(2008\)](#)
 Gulf of Maine – [Charette et al. \(2001\)](#), [Newell et al. \(2005\)](#), [Pilskaln et al. \(2014\)](#)
 Cape Lookout Bight, North Carolina – [Shanks \(2002\)](#)
 Northern Gulf of Mexico continental shelf – [Rabalais et al. \(2001\)](#)
 Southern Indian Ocean – [Møller et al. \(2011\)](#)
 Central Benguela System – [Romero et al. \(2002\)](#)
 Southeast Atlantic – [Lončarić et al. \(2007\)](#)
 Subarctic/temperate North Pacific – [Andreev et al. \(2002\)](#), [Honda et al. \(2002, 2013\)](#), [Kawahata \(2002\)](#), [Shin et al. \(2002\)](#), [Wong and Crawford \(2002\)](#)
 North Pacific – [Bishop and Wood \(2008\)](#), [Buesseler et al. \(2009\)](#), [Jackson and Checkley \(2011\)](#), [Kahn et al. \(2012\)](#), [Kawakami and Honda \(2007\)](#), [Moeseneder et al. \(2012\)](#), [Petrík et al. \(2013\)](#), [Ruhl et al. \(2008\)](#), [Saino et al. \(2004\)](#), [Smith Jr. et al. \(2006a, 2006a, 2008a, 2008b, 2008c, 2009, 2013a, 2013b, 2014a, 2014b\)](#), [Vardaro et al. \(2009\)](#), [Wilson et al. \(2013\)](#), [Yamamoto et al. \(2007\)](#), [Yu et al. \(2001\)](#)
 Sagami Bay, Japan – [Masuzawa et al. \(2003\)](#), [Nakatsuka et al. \(2003a, 2003b\)](#)
 Oura Bay, Japan – [Itoh et al. \(2007\)](#)
 Kagoshima Bay, Japan – [Kobari et al. \(2010\)](#)
 Kuroshio Extension – [Takahashi et al. \(2013\)](#)
 Santa Barbara Channel, California – [Goldthwait and Alldredge \(2006\)](#), [Passow et al. \(2006\)](#)
 Santa Barbara Basin, California – [Sekula-Wood et al. \(2009, 2011\)](#), [Shipe et al. \(2002\)](#)
 San Pedro Basin, California – [Collins et al. \(2011\)](#), [Schnetzer et al. \(2007\)](#)
 California Current Ecosystem – [Stukel et al. \(2011, 2013a\)](#)
 Juan de Fuca Ridge – [Cowen et al. \(2001\)](#)
 British Columbia, Canada – [Timothy \(2004\)](#), [Timothy et al. \(2003\)](#)
 East China Sea – [Guo et al. \(2010\)](#), [Iseki et al. \(2003\)](#), [Liu et al. \(2003\)](#)
 SW Pacific Ocean – [Sikes et al. \(2005\)](#)
 Northern Chile – [González et al. \(2004, 2007, 2009\)](#), [Grunewald et al. \(2002\)](#), [Pantoja et al. \(2004\)](#)
 Chilean Patagonian fjords – [González et al. \(2010, 2011, 2013\)](#)
 Eastern Indian Ocean – [Okubo et al. \(2007\)](#)
- Tropic/subtropic*
- Arabian Sea – [Berelson \(2001, 2002\)](#), [Borole \(2002\)](#), [Gauns et al. \(2005\)](#), [Hansell and Ducklow \(2003\)](#), [Mincks et al. \(2000\)](#), [Primeau \(2006\)](#), [Ramaswamy et al. \(2005\)](#), [Rixen et al. \(2005\)](#), [Roman et al. \(2000\)](#), [Singh and Conan \(2008\)](#), [Stoll et al. \(2007a\)](#), [Yu et al. \(2001\)](#)
 Bay of Bengal – [Gauns et al. \(2005\)](#), [Stoll et al. \(2007b\)](#), [Unger et al. \(2003\)](#)
 Bermuda Atlantic Time-series Study (BATS) – [Amacher et al. \(2013\)](#), [Brix et al. \(2006\)](#), [Buesseler et al. \(2008a\)](#), [Church et al. \(2013\)](#), [Conte and Weber \(2014\)](#), [Conte et al. \(2003\)](#), [Estapa et al. \(2013\)](#), [Helmke et al. \(2010\)](#), [Hong et al. \(2013\)](#), [Karl et al. \(2001b\)](#), [Lomas and Bates \(2004\)](#), [Lomas et al. \(2010\)](#), [Lomas et al. \(2013\)](#), [McGillicuddy Jr. et al. \(2007\)](#), [Neuer et al. \(2002b\)](#), [Owens et al. \(2013\)](#), [Roman et al. \(2002\)](#), [Schnetzer and Steinberg \(2002\)](#), [Shatova et al. \(2012\)](#), [Stanley et al. \(2004, 2012\)](#), [Steinberg et al. \(2002, 2012\)](#), [Stewart et al. \(2010\)](#), [Sweeney et al. \(2003\)](#)
 Sargasso Sea – [Brew et al. \(2009\)](#), [Goldthwait and Steinberg \(2008\)](#), [Krause et al. \(2009\)](#), [Lomas et al. \(2009a, 2009b\)](#), [Maiti et al. \(2009\)](#), [Ono et al. \(2001\)](#), [Stoll et al. \(2007a\)](#)
 Azores – [Huskin et al. \(2004\)](#)
 Canary Islands – [Neuer et al. \(2002a, 2002b, 2007\)](#)
 Subtropical North Atlantic – [Baltar et al. \(2009\)](#)
 North and South Atlantic gyres – [Thomalla et al. \(2006\)](#)
 Off Mauritania – [Bory et al. \(2001\)](#), [Fischer and Karakaş \(2009\)](#), [Iversen et al. \(2010\)](#)
 Cariaco Basin (CARIACO) – [Benitez-Nelson et al. \(2007b\)](#), [Church et al. \(2013\)](#), [Goñi et al. \(2003\)](#), [Goni et al. \(2009\)](#), [Montes et al. \(2012, 2013\)](#), [Taylor et al. \(2009\)](#), [Woodworth et al. \(2004\)](#)
 Gulf of Mexico – [Hung et al. \(2004, 2010b\)](#), [Santschi et al. \(2003\)](#)
 Gulf of California and eastern tropical North Pacific – [Silverberg et al. \(2014\)](#), [White et al. \(2013\)](#), [Wolhowe et al. \(2014\)](#)
 Costa Rica upwelling dome – [Stukel et al. \(2013b\)](#)
 Hawaii Ocean Time-series (HOT) – [Bidigare et al. \(2009\)](#), [Boyd et al. \(2008\)](#), [Brix et al. \(2004, 2006\)](#), [Buesseler et al. \(2007b, 2008b\)](#), [Church et al. \(2013\)](#), [Corno et al. \(2007\)](#), [Dore et al. \(2002, 2008\)](#), [Hannides et al. \(2009\)](#), [Karl et al. \(2001a, 2001b\)](#), [Keeling et al. \(2004\)](#), [Lamborg et al. \(2008\)](#), [Neuer et al. \(2002b\)](#), [Prahl et al. \(2005\)](#), [Roman et al. \(2002\)](#), [Smith Jr. et al. \(2002\)](#), [Steinberg et al. \(2008a, 2008b\)](#), [Trull et al. \(2008b\)](#), [Wilson and Steinberg \(2010\)](#), [Wilson et al. \(2008, 2010\)](#)
 Hawaii – [Benitez-Nelson et al. \(2007a\)](#), [Estapa et al. \(2013\)](#), [Landry et al. \(2008\)](#), [Maiti et al. \(2008\)](#), [Rii et al. \(2008\)](#), [Siegel et al. \(2008\)](#), [Verdeny et al. \(2008\)](#)
 Subtropical Northwest Pacific – [Hung et al. \(2009, 2010c, 2012\)](#), [Kim et al. \(2014\)](#), [Kobari et al. \(2013\)](#)
 Equatorial Pacific – [Armstrong et al. \(2002\)](#), [Berelson \(2001\)](#), [Brown et al. \(2001\)](#), [Kim et al. \(2011, 2012\)](#), [Murray et al. \(2005\)](#), [Primeau \(2006\)](#), [Rontani et al. \(2011\)](#), [Sheridan et al. \(2002\)](#)
 Eastern Tropical South Pacific – [Haskell II et al. \(2013\)](#)
 South Pacific – [Guidi et al. \(2008\)](#), [Twining et al. \(2014\)](#)
 South China Sea – [Cai et al. \(2002\)](#), [Hung et al. \(2010a\)](#), [Lahajnar et al. \(2007\)](#)
 Equatorial Indian Ocean – [Vidya et al. \(2013\)](#)
 Basin-wide – Atlantic Ocean – [Antia et al. \(2001\)](#)
 Global – [Berelson et al. \(2007\)](#), [Boyd et al. \(2007\)](#), [Buesseler et al. \(2006\)](#), [Henson et al. \(2012b\)](#), [Honjo et al. \(2008\)](#), [Howard et al. \(2006\)](#), [Lam et al. \(2011\)](#), [Lutz et al. \(2002, 2007\)](#)

in POC flux attenuation at the two sites were not primarily due to the amount of POC flux, but rather to the types of phytoplankton that produced the exported POC.

Buesseler and Boyd (2009) compared several areas of the ocean in terms of metrics representing net primary productivity, export flux through the bottom of the euphotic zone and attenuation of export flux in the upper mesopelagic zone. The areas and times that were compared included Station K2 in the subarctic North Pacific in summer (Boyd et al., 2008; Buesseler et al., 2007b, 2008b; Lamborg et al., 2008; Steinberg et al., 2008a), Station ALOHA in the subtropical North Pacific in summer (Boyd et al., 2008; Buesseler et al., 2007b, 2008b; Lamborg et al., 2008; Steinberg et al., 2008a), the northeast North Atlantic during the spring bloom (Buesseler et al., 1992), the equatorial Pacific during spring and fall (Bacon et al., 1996), the Southern Ocean just south of the Antarctic Polar Front during austral summer (Buesseler et al., 2001, 2003), and the subarctic northeastern North Pacific during spring and summer (Charette et al., 1999). There were pronounced differences in primary productivity, export flux and flux attenuation in these studies. During the spring bloom in the North Atlantic and in the Southern Ocean, there was high net primary productivity and high export of large diatoms sinking out of the euphotic zone. In the North Atlantic there was little or no attenuation of the flux even at the bottom of the mesopelagic zone, but in the Southern Ocean there was a shift from high to lower mesopelagic export attenuation within only a month. In the northwestern subarctic Pacific, there was also high net primary productivity, but somewhat reduced export from the euphotic zone, due to a shift from large diatoms that had caused the spring/early summer bloom, to smaller cells in the late summer. In the northeastern subarctic Pacific, there was high primary production, but low export from the euphotic zone and high flux attenuation in the upper mesopelagic. This system was dominated by nanoplankton <5 µm in size, which were being heavily grazed. Both the subtropical North Pacific off Hawaii and the equatorial Pacific had low export from the euphotic zone into the upper mesopelagic. However these stations differed in net primary productivity, with low productivity off Hawaii but high productivity in the equatorial Pacific. Both of these systems were characterized by picoplankton, which were efficiently grazed by microzooplankton and small mesozooplankton.

Variations in export flux from the euphotic zone, and attenuation in the mesopelagic zone can be due to sedimentation pulses in response to episodic events in the overlying water column. Included are biological events such as blooms of diatoms (Dore et al., 2008; Lalande et al., 2011; Martin et al., 2011; Michels et al., 2008; Rynearson et al., 2013; Thompson et al., 2008), *Phaeocystis* spp. (Lalande et al., 2011; Michels et al., 2008), or other phytoplankton (Buesseler et al., 2010; Karl et al., 2012). Episodic export has also followed blooms triggered by physical forcing such as wind events (Pesant et al., 2002), winter or spring storms (Koeve et al., 2002; Lomas et al., 2009a, 2009b; Lopez-Fernandez et al., 2013a), hurricanes (Conte, M., data shown in Fig. 4 of Ducklow et al., 2009), typhoons (Hung et al., 2010c), and passage of eddies through various locations including the Sargasso Sea (Buesseler et al., 2008a; Conte et al., 2003; Goldthwait and Steinberg, 2008; McGillicuddy et al., 2007; Shatova et al., 2012; Sweeney et al., 2003), the Arctic Ocean (Lalande et al., 2011; O'Brien et al., 2013), and off Hawaii (Benitez-Nelson et al., 2007a; Emerson et al., 2001; Landry et al., 2008; Ri et al., 2008; Verdeny et al., 2008). Physical events such as those mentioned above enhance export of particles and chemicals by causing vertical mixing which injects nutrients into the euphotic zone from below, stimulating phytoplankton blooms which then sink.

Variations in export flux due to biological and physical phenomena may have contributed to major imbalances between measured export flux of POC out of the epipelagic zone and estimated demands for organic carbon by heterotrophic food webs at mesopelagic and

deeper depths (Baltar et al., 2009; Burd et al., 2010, and references therein). POC in export flux would be utilized at depth by combinations of microbial decomposition, solubilization and detritivorous feeding by zooplankton. Reinthaler et al. (2006) estimated that the prokaryote carbon demand (PCD) in the North Atlantic exceeded POC flux by two orders of magnitude. Steinberg et al. (2008b) found that mesopelagic PCD was 3 times higher than POC flux in the subtropical Pacific, and 10 times higher in the subarctic Pacific. Uchimiya et al. (2013) estimated that PCD exceeded POC flux by 38 times in the Canada Basin of the western Arctic.

Suggested reasons for imbalances between carbon demand and POC flux have included several factors that underestimate the true supply of POC exported to depth. There may be failure to account for additional POC delivered by lateral intrusion of external water masses (Uchimiya et al., 2013), or suspended small particles of POC that are not captured by sediment traps (Verdugo et al., 2004; Baltar et al., 2009; Burd et al., 2010). There are abundant sub-micrometer- to centimeter-sized buoyant small particles suspended throughout the water column with no apparent decreases in abundance with depth (Abramson et al., 2010; Herndl and Reinthaler, 2013; Goutx et al., 2007). These particles are one to two orders-of-magnitude more abundant than particles captured by sediment traps (Baltar et al., 2009), and these suspended small particles may be extensively degraded by microbes (Riley et al., 2012) and closely linked to microbial processes in the deep ocean (Baltar et al., 2009). Macroscopic particles (>500 µm) may also be buoyant (Bohdansky et al., 2010), and thus not captured by sediment traps.

There may also be underestimation of the delivery of POC to sediment traps during episodic events, because sediment traps integrate periods of weeks to months, but episodic events can occur on time scales of days (Hansell and Ducklow, 2003; Karl et al., 2003; Lomas et al., 2013). Included would be massive ephemeral blooms of gelatinous zooplankton that are difficult to sample (Herndl et al., 2008). Estapa et al. (2013) found high variability in particle flux over timescales of approximately a day in the western Sargasso Sea and the subtropical North Pacific. There can also be underestimation of POC in sediment traps due to solubilization of POC particles to DOC, which is not recovered (Antia, 2005a).

There may also be additional delivery of POC to depth by other mechanisms. Included are active transport of carbon by vertically-migrating zooplankton, which is not accounted for by sediment traps (Steinberg et al., 2008a). Part of the carbon demand may also be met by convective mixing of dissolved organic carbon (DOC) from the euphotic zone which may help support heterotrophic metabolism at depth (Arístegui et al., 2002; Carlson et al., 2010; Hansell et al., 2012), or by chemoaautotrophy by prokaryotes in the deep oxygenated water column, which converts inorganic carbon to organic carbon (Anantharaman et al., 2013; Herndl et al., 2005; Ingalls et al., 2006b; Reinthaler et al., 2010; Swan et al., 2011). Thus, microbial conversion of inorganic carbon to organic matter in the water column of the deep ocean, together with additional POC in suspended particles that are not well captured by sediment traps, may help to narrow the imbalances between organic supply to, and demand in the deep sea (Herndl and Reinthaler, 2013).

Some of the imbalances between POC exported to depth and estimated microbial metabolic demands at depth may stem from misunderstanding of the abundance and activity of deep-sea microbial communities (Herndl and Reinthaler, 2013). Microbes attached to particles in the deep sea are more abundant than free-living microbes in the water (Arístegui et al., 2009; Cho and Azam, 1988; DeLong et al., 2006), and particle-associated microbes in the deep sea are phylogenetically and functionally different from each other (Eloe et al., 2010), and from those that occur near the

surface in terms of responses to pressure (Grossart and Gust, 2009; Tamburini et al., 2006, 2013). Since most estimates of microbial activity in the deep sea have been based on measurements under surface pressure conditions (Herndl and Reinhäler, 2013), some of these estimates may be incorrect. It is unknown whether most deep-sea microbes have reduced metabolism in response to pressure, in which case deep-sea microbial metabolism may have been overestimated, or the reverse (Nagata et al., 2010; Tamburini et al., 2013). What is becoming clear is that deep-sea microbial communities are fundamentally different from those near the surface (Herndl and Reinhäler, 2013; Nagata et al., 2010).

In an attempt to reconcile such imbalances between supply of POC through export flux with respiration demands of mesopelagic biota, Anderson and Tang (2010) modeled turnover of sinking detrital POC through its respiration by (1) colonization of detritus by attached bacteria, (2) production of bacterioplankton using dissolved organic carbon from particle degradation, and (3) consumption by zooplanktonic detritivores. The model suggested that bacteria (both attached and free-living) accounted for 84.7% of respiration, and that bacteria were the main sink for POC supplied to the mesopelagic zone. Zooplankton detritivores accounted for only 6.6% of total respiration, and mainly recycled carbon in detritus back into fecal pellets and DOC.

A model by Gehlen et al. (2006) suggested that different processes control fluxes of POC at different depths. In the upper wind-mixed layer, turbulent coagulation of particles appeared to be an important process. Below the wind-mixed layer, POC fluxes were most sensitive to flux feeding and repackaging by zooplankton. The model also suggested that formation of aggregates was important to promote a substantial biological pump, but the constant particle fluxes at deep depths were likely due to combined effects of aggregate formation and mineral ballasting.

Understanding of balances between supply and demand of organic materials in the deep sea depends upon the accuracy of measurements of export flux. However, the two primary means to measure POC flux from the epipelagic, sediment traps and ^{234}Th budgets, frequently disagree (Benitez-Nelson and Charette, 2004; Haskell II et al., 2013). In a comparison of export fluxes measured by sediment traps and thorium-based methods, Haskell II et al. (2013) found that the thorium-based methods produced higher fluxes than sediment traps, except in cases where most of the export flux was due to heavily-ballasted diatoms. Haskell II et al. (2013) concluded that sediment traps undercollected small poorly-ballasted slowly-sinking particles that carried most of the ^{234}Th at most stations. However, the accuracy of thorium-based methods varies with sizes of particles in sinking assemblages, and whether particles settle as single cells or as flocculated assemblages (Smith et al., 2006a, 2006b; Waite and Hill, 2006).

The extent to which sediment traps and other techniques accurately measure export flux is still unclear. Antia (2005a) noted (p. 190) that “*Almost simultaneous with the enthusiasm in deploying traps in numerous environments came the sobering realization that they fell short of collecting the “true” sinking flux...*”. More simultaneous comparisons of collection efficiency of sediment traps, polyacrylamide gel traps, and thorium-based methods are clearly needed. For instance, Ebersbach and Trull (2008) found that carbon fluxes recorded for polyacrylamide gel traps were 3–4 times higher than those for POC fluxes from sediment traps, and these authors speculated that the higher values were due to overestimates of carbon fluxes in the gel traps due to the volume-to-carbon conversions used for the gel traps. Estimates of carbon flux at 100 m depth based on ^{234}Th methods in the study of Ebersbach and Trull (2008) were higher than those from gel traps at some stations, but similar at other stations. Ebersbach and Trull (2008) suggested that these differences may have been due to differences in carbon contents in aggregates versus fecal pellets comprising the

dominant particles at different stations, or that the flux measured over short time periods for the gel traps may have been lower than that recorded by the ^{234}Th methods, which integrated flux over the previous few weeks.

Henson et al. (2011) compared estimates of export flux by ^{234}Th methods with those obtained from satellite-derived primary productivity, nutrient *f*-ratio, and sea surface temperature data (Lawson et al., 2000), and found that there were major discrepancies. Henson et al. (2011) discussed the reasons for such inconsistency, and concluded that the lack of consensus for estimates of export through the biological pump emphasizes that our knowledge of planetary carbon flux remains incomplete.

Giering et al. (2014) used field data, respiration-rate estimates and a model to attempt reconciliation of the carbon budget of the mesopelagic zone (50–1000 m) in the eastern North Atlantic. By making several assumptions, the carbon sources and sinks were balanced to within observational uncertainties. The upper limit of the mesopelagic zone used in the estimations was 50 m, which was the mixed-layer depth throughout most of the study. Zooplankton resident in the mesopelagic zone were used for respiration estimates, but vertically-migrating zooplankton were excluded from estimates because migrators were assumed to ingest sufficient carbon while in the epipelagic to satisfy their demands while in the mesopelagic. Estimates of carbon utilization also compared respiration rather than carbon demand to net organic carbon supply as measured by sediment traps. Results indicated that prokaryotes were responsible for 70–92% of the estimated remineralization of carbon in the mesopelagic zone. This was despite the fact that much of the organic carbon was exported into the mesopelagic zone as large, fast-sinking particles that could be ingested by larger zooplankton. Giering et al. (2014) suggested that zooplankton fragmented and ingested approximately half of these particles, of which >30% per day were released as suspended and slowly-sinking particles that were utilized by microbes. These authors concluded that the “synergy between zooplankton and microbes in the twilight zone” were important in processing the organic carbon flux, and in controlling the oceanic carbon sink.

Dissolved organic carbon (DOC)

Transport of DOC to depth by vertical mixing can be an important component of the biological pump. There is a huge pool of DOC in the ocean (Hopkinson Jr. and Vallino, 2005), which is a global average of 17% of global new primary production (Hansell and Carlson, 1998). DOC interacts with POC exported through the biological pump (Stone, 2010; Jiao et al., 2010; Jiao and Azam, 2011). DOC is transported to depth primarily by vertical mixing of water and may constitute 9–20% of the biological pump in the North Atlantic (Carlson et al., 2010; Hansell et al., 2009). The biological pump deposits about 0.3 billion tons of carbon each year to the deep sea in particulate form, but about 700 billion tons is dissolved in the water column as DOC. The DOC in the ocean is more than the 600 billion tons of carbon in all land biomass combined, and almost as much as the 750 billion tons of carbon in atmospheric CO₂ (Stone, 2010). Approximately 95% of the dissolved organic matter (DOM) in the ocean is refractory (or recalcitrant) dissolved organic matter (RDOM), in that it cannot be used as food by marine organisms (Hansell, 2013). The RDOM is produced by what Jiao et al. (2010) called the “microbial carbon pump” (MCP), by which bioavailable DOC is converted by marine microbes into RDOM (Kolber et al., 2001; Ogawa et al., 2001). Thus, marine microbes are accounting for massive redistributions of carbon that will affect the global carbon cycle, particularly as it responds to climate change (Jiao and Azam, 2011). Pedler et al. (2014) have recently shown that a commonly-recorded single strain of the bacterial genus *Alteromonas* has the ability to consume the entire pool of

labile DOC in coastal waters, further attesting to the disproportionate role of certain bacteria in altering the fate of carbon in the sea.

Whether the ocean overall produces more carbon through primary production than is used through respiration is a key to understanding the global carbon cycle. The question of whether ocean metabolism is net autotrophic or heterotrophic has been a subject of active debate for over a decade (del Giorgio and Duarte, 2002; Regaudie-de-Gioux and Duarte, 2013; Ducklow and Doney, 2013; Williams et al., 2013; Duarte et al., 2013, and references therein). There are indications that carbon respiration may exceed production over much of the ocean, particularly in oligotrophic areas, for most of the time. Although studies of the biological pump have been primarily focused on POC flux to depth, most of the respiration of heterotrophic planktonic bacteria is supported by DOC (del Giorgio and Duarte, 2002). Thus, estimates of respiration based primarily on POC fluxes may underestimate total fluxes by not including the contribution of respiration supported by DOC. Stoichiometry of C:N:P of DOM (199:20:1) is substantially greater than the Redfield ratios (106:16:1), possibly contributing to the excess respiration estimated for the deep ocean (Hopkinson Jr. and Vallino, 2005). Since DOC may be based on primary production that occurred thousands of years ago, then ancient DOC may be supporting contemporary microbial respiration, which is greater at times than that which could be supported by contemporary primary productivity (del Giorgio and Duarte, 2002).

Much of the debate over net autotrophy versus heterotrophy revolves around advantages and limitations of incubation (*in vitro*) versus incubation-free (*in situ*) methods to measure both primary production and net plankton community metabolism (Ducklow and Doney, 2013; Williams et al., 2013; Duarte et al., 2013). These issues are currently unresolved, but are important for understanding the global carbon budget, particularly in view of predicted responses to changing climate in the near future.

Zooplankton fecal pellets

Contribution of zooplankton fecal pellets to export flux

Zooplankton fecal pellets are an important but highly-variable component of the POC export to depth. Different components of zooplankton communities produce different types and sizes of fecal pellets. Included are “minipellets” produced by protistan microzooplankton such as heterotrophic dinoflagellates, ciliates and radiolarians, as well as minute metazoans such as copepod nauplii and small copepodites (Beaumont et al., 2002; Gowing and Silver, 1985); cylindrical or ovoid fecal pellets produced by copepods (Beaumont et al., 2002; Gleiber et al., 2012; Köster et al., 2011); larger fecal strings produced by euphausiids (Atkinson et al., 2012; Gleiber et al., 2012); and tabular fecal flakes produced by salps, appendicularians and other tunicates (Gleiber et al., 2012; Phillips et al., 2009). These different sizes and types of fecal pellets have different densities and sinking rates, and can contribute differentially to the export versus retention of fecal pellet components in various layers of the water column.

The proportion of the estimated overall sinking particulate carbon flux contributed by recognizable zooplankton fecal pellets is highly variable (<1–>100% – Table 2), with most values <40% (Dubischar and Bathmann, 2002; Ducklow et al., 2001; Fortier et al., 2002). Variation in phytoplankton and zooplankton biomass and community composition can have substantial effects on the magnitude of fecal pellet export of POC to depth. Also, the relative contributions of other components of the biological pump, such as marine snow and phytodetrital aggregates, can affect the proportion of the total POC flux attributed to zooplankton fecal pellets (Wilson et al., 2013). For instance, in the California Current

Ecosystem Stukel et al. (2013a) found that zooplankton fecal pellets comprised a higher proportion of the total passive particulate export (up to 94%) during the productive spring period, but much lower proportions of total passive flux (as little as 1.9%) during the fall, when vertical fluxes contained higher proportions of marine snow and unidentifiable particles. Also, collection method can cause variation in the fraction of export flux attributed to fecal pellets. Ebersbach and Trull (2008) found that polyacrylamide gels in sediment traps reduced disaggregation of particles in sediment traps, resulting in high amounts of recognizable fecal pellets in sediment traps.

A compilation by Wilson et al. (2013) of data for total POC flux and fecal pellet percentage of total POC flux from numerous studies and sites revealed that these two parameters were not significantly correlated for epipelagic and mesopelagic depths, or for most bathypelagic depths. However, there was a significant correlation for certain bathypelagic depths, driven largely by the data of Shatova et al. (2012) from BATS. Wilson et al. (2013) noted that the general decline in the proportion of total POC attributable to fecal pellet POC as total POC increased, and suggested that periods of high total POC flux were dominated by contributions from non-fecal-pellet sources of POC, such as as marine snow or phytodetritus. Indeed, phytodetrital aggregates were visible on the seafloor during periods of high total POC export flux in the northeast Atlantic (Bett et al., 2001) and the northeast Pacific (Smith Jr. et al., 2008a, 2008b, 2008c). Conversely, Wilson et al. (2013) found that during periods of lower overall POC fluxes, the contribution of fecal pellet POC increased, both at their station in the northeast Pacific, and at other sites, based on their compilation of data from the literature. Wilson et al. (2013) suggested that this negative correlation between total POC flux and fecal pellet POC flux to depth may be a common feature of deep-sea fluxes.

Epipelagic retention of zooplankton fecal pellets due to zooplankton activities

Most zooplankton fecal pellets produced at epipelagic depths appear to be recycled by the activities of other zooplankters. A common observation in many sediment-trap studies of POC export is that most of the zooplankton fecal pellets calculated to have been produced in the upper hundred meters or so of the epipelagic zone do not appear to sink very far below it (Viitasalo et al., 1999; Wexels Riser et al., 2001, 2002, 2007). This suggests that fecal pellets are being recycled or otherwise retained in the epipelagic. However, relative to rates of microbial decomposition, most measured fecal-pellet sinking velocities are fast enough (hundreds of meters per day) for fecal pellets to descend below the epipelagic before becoming remineralized by microbes (Turner, 2002). This has led to suggestions that much of the epipelagic retention of fecal pellets is due to activities of other zooplankters, primarily copepods (González and Smetacek, 1994). Such activities include ingestion of entire fecal pellets (coprophagy), being broken up into smaller particles (coprorhexy) or disruption of the pellet peritrophic membranes resulting in partial dispersal of pellet contents into the water (coprochaly) (Lampitt et al., 1990). All of these activities would be expected to change larger rapidly-sinking particles into smaller suspended ones, thereby retaining fecal materials in the epipelagic and retarding their transport to depth. Such retention of fecal pellets may range from 30% to 98% (Svensen et al., 2012).

Based on limited experimental evidence, González and Smetacek (1994) suggested that the cyclopoid copepod *Oithona similis* ingests fecal pellets of several calanoid copepod species. The ubiquitous abundance of *O. similis* in the ocean may provide a “coprophagous filter” to retain many copepod fecal pellets in the epipelagic. *O. similis* does not produce a feeding current like most calanoid copepods, but rather it feeds as an ambush-predator,

Table 2

Zooplankton fecal pellet contribution to total particulate organic carbon flux.

Location	Depth	Fecal pellet%	Reference
Various	Various	<1->100	22 papers cited in Turner (2002)
Arctic Ocean	30–200 m	<2	Olli et al. (2007)
Greenland Sea, Fram Strait, and Barents Sea	470–3000 m	<24	Tameler et al. (2012)
Barents Sea	Upper 200 m	8–40	Wexels Riser et al. (2002)
Barents Sea	Upper 200 m	1–37	Wexels Riser et al. (2007)
Barents Sea	Upper 200 m	13–27	Wexels Riser et al. (2008)
Fram Strait	340 m	10–>85	Lalande et al. (2011)
Fram Strait	179–280 m	<15–29	Lalande et al. (2013)
Balsfjord, Norway	Upper 100 m	7–75	Wexels Riser et al. (2010)
Disko Bay, Greenland	Upper 100 m	29	Juul-Pedersen et al. (2006)
Baffin Bay, Canada	Upper 200 m	1–63	Sampei et al. (2004)
Hudson Bay, Canada	50 m	52	Lapoussière et al. (2009)
Barrow Strait, Canada	Upper 90 m	<10–37	Fortier et al. (2002)
Beaufort Sea, Canada	50 m	2.4–75.7	Juul-Pedersen et al. (2010)
Newfoundland, Canada	40–240 m	20–>90	Thompson et al. (2008)
Scotian Shelf	50–150 m	4–50	Caron et al. (2004)
Iberian shelf	50–200 m	>20 (on-shelf)	Wexels Riser et al. (2001)
Iberian shelf	50–200 m	0.3–6.7 (off-shelf)	Wexels Riser et al. (2001)
Azores	200 m	2–82	Huskin et al. (2004)
Sargasso Sea	500 m	0.4–10	Shatova et al. (2012)
Sargasso Sea	1500 m	3–16	Shatova et al. (2012)
Sargasso Sea	3200 m	1.4–8	Shatova et al. (2012)
Sargasso Sea	150 m	28–89	Steinberg et al. (2012)
Sargasso Sea	150–300 m	5–12 (inside eddies)	Goldthwait and Steinberg (2008)
Sargasso Sea	150–300 m	4–7 (outside eddies)	Goldthwait and Steinberg (2008)
Northern Gulf of Mexico	60 m	55	Rabalais et al. (2001)
Aegean Sea	16 m	10–53	Frangoulis et al. (2010)
Northwest Mediterranean	200–800 m	18–87	Abramson et al. (2010)
Bay of Calvi	36 m	<6	Frangoulis et al. (2011)
Central North Pacific	150–500 m	14–35	Wilson et al. (2008)
Northwest Pacific	150–500 m	3–39	Wilson et al. (2008)
Kagoshima Bay, Japan	50 and 150 m	<4->40%	Kobari et al. (2010)
Northeast Pacific	3500 m	3.3–47.7	Wilson et al. (2013)
California Current	100 m	1.9–94	Stukel et al. (2013a)
Chilean upwelling	2300 m	17–44	González et al. (2004)
Chilean upwelling	50 m	79.6	González et al. (2007)
Chilean upwelling	50–100 m	61–90	González et al. (2009)
Southern Ocean	100 m	2–7 (summer)	Dagg et al. (2003)
Southern Ocean	100 m	22–63 (spring)	Dagg et al. (2003)
Ross Sea	200 m	<1->50	Smith et al. (2011)
Terra Nova Bay (Ross Sea)(<i>Limacina helicina</i> fp only)	180 m	10–30	Manno et al. (2010)
Antarctic Peninsula shelf	170 m	34–67	Gleiber et al. (2012)

hanging motionless in the water until responding to hydromechanical cues from prey motion or sinking fecal pellets (Kiørboe and Visser, 1999; Svensen and Kiørboe, 2000). Thus, this copepod could potentially be an important part of a copepod coprophagous filter for sinking copepod fecal pellets. There is evidence from mesocosm studies that *Oithona* sp. may be important consumers of fecal pellets of calanoid copepods (Svensen and Nejstgaard, 2003), in that there was a significant negative correlation between vertical flux of fecal pellet carbon and *Oithona* sp. biomass. Several recent sediment-trap studies of vertical distributions of fecal pellets have also provided support for the copepod coprophagous filter hypothesis (examples include Wexels Riser et al., 2001, 2002, 2007; Dubischar and Bathmann, 2002; Suzuki et al., 2003; Huskin et al., 2004; Sampei et al., 2004, 2009b; Juul-Pedersen et al., 2006). Other copepods have also been circumstantially implicated as consumers or destroyers of zooplankton fecal pellets and other detrital particles, including copepods of the genus *Oncaeae* (Møller et al., 2011) and pelagic harpacticoids such as *Microsetella norvegica* (Koski et al., 2005, 2007).

Recent studies have questioned the importance of a coprophagous filter involving copepods of the genus *Oithona*. Reigstad et al. (2005) found no evidence for feeding of *Oithona* spp. (mainly *O. similis*) on fecal pellets produced by *Calanus finmarchicus*. Reigstad et al. (2005) suggested that the feeding of *O. similis* on fecal pellets of other copepod species recorded for the experiments of González and Smetacek (1994) may have been because the latter

experiments were conducted in upright containers where fecal pellets had sunk to the container bottoms and *O. similis* were observed feeding on fecal pellets from the bottoms of containers. When Reigstad et al. (2005) performed experiments in rotating containers, thereby more closely simulating conditions of copepods feeding in the sea, no feeding on fecal pellets by *Oithona* spp. were recorded.

Copepods other than *Oithona* spp. have been shown to ingest fecal pellets from other copepods (Poulsen and Kiørboe, 2005, and references therein). However, such fecal pellet ingestion may be incidental. Poulsen and Kiørboe (2005) found that the calanoid copepods *Acartia tonsa* and *Temora longicornis* ingested their own fecal pellets, but that the presence of alternative phytoplankton food increased the rates of feeding on fecal pellets. In the absence of alternative phytoplankton food, copepods did not create a feeding current, and few fecal pellets were ingested. However, in the presence of alternative phytoplankton food, copepods switched to suspension feeding with a feeding current, and fecal pellets were ingested along with phytoplankton, perhaps unintentionally. Poulsen and Kiørboe (2005) also found that clearance rates for copepods feeding on fecal pellets decreased with increasing fecal pellet size. Since copepod fecal pellet size is related to type of food ingested to form the fecal pellets, and diatom diets have been shown to produce larger fecal pellets (Besiktepe and Dam, 2002), coprophagy of copepod fecal pellets by other copepods would be expected to diminish with larger fecal pellets. Poulsen and

Kørboe (2005) found that 95% of the intact or fragmented fecal pellets caught in copepod feeding appendages were actively rejected, and that such rejection could cause further damage to fecal pellets. Similarly, Iversen and Poulsen (2007) found that the copepods *Oithona similis*, *Calanus helgolandicus* and *Pseudocalanus elongatus* ingested fecal pellets both in the absence and presence of alternative phytoplankton food, but that ingestion of fecal pellets was higher in the presence of alternative food. Most fecal pellet ingestion by the calanoids *C. helgolandicus* and *P. elongatus* appeared to be unintentional ingestion of small fecal pellet fragments, during suspension feeding on phytoplankton. Most fecal pellets were rejected by these two copepods, with pellets becoming damaged during the rejection process. Thus, Poulsen and Kørboe (2005) and Iversen and Poulsen (2007) concluded that the main effect of copepods in reducing the vertical flux of fecal pellets may be through coprophagy rather than coprophagy, with copepods damaging fecal pellets while rejecting them, and turning large fecal pellets into smaller fecal fragments that sink more slowly, and are more subject to microbial degradation.

Much of the epipelagic degradation of copepod fecal pellets may be accomplished by plankton other than copepods. Poulsen and Kørboe (2006) found that in the North Sea in summer, only 3–39% of the fecal pellets produced in the upper 50 m of the water column were collected in sediment traps at 50 m depth. Most of the fecal pellet degradation was due to organisms <200 µm in size. The copepod community was dominated by *Oithona similis*, and shipboard coprophagy experiments suggested that degradation of fecal pellets through coprophagy by *O. similis* and other copepods would be three orders-of-magnitude lower than estimated total fecal pellet degradation in the upper 50 m of the water column. Thus, Poulsen and Kørboe (2006) concluded that copepods were not the primary agents in retarding the vertical flux of their own fecal pellets, and that microzooplankton <200 µm in size were important in degradation of fecal pellets in the epipelagic.

The importance of microzooplankton in the degradation of copepod fecal pellets was confirmed by Poulsen and Iversen (2008). Total copepod fecal pellet removal rates in a seasonal study in Danish coastal waters ranged from 22% d⁻¹ in July to 87% d⁻¹ in May. Protozooplankton, primarily dinoflagellates and ciliates 20–100 µm in size, were the primary agents of fecal pellet degradation. These protists accounted for 15–53% of total fecal pellet degradation rates. Indeed, microscopic observations confirmed that heterotrophic dinoflagellates such as *Gyrodinium dominans*, *G. spirale*, and *Protoperdinium* spp. could feed upon fecal pellets, and that dinoflagellates were more important than ciliates in fecal pellet degradation. Free-living bacteria (0.2–2 µm in size) in the natural water did not contribute substantially to fecal pellet degradation, but culture-originating bacteria (<0.2 µm in size) that were associated with copepod fecal pellets, which were introduced to incubations, accounted for up to 2–59% of total fecal pellet degradation. Mesozooplankton >200 µm in size did not contribute significantly to fecal pellet degradation, although late-stage copepod nauplii may have been sporadically important during 3 months of the experiment. Although copepods >200 µm in size were not important as direct agents in the degradation of fecal pellets, they may have been indirectly important because they fed heavily on the protozooplankton that were the primary pellet degraders. Such an effect was indicated during July when high copepod abundances coincided with low protozooplankton abundances, and low fecal pellet degradation rates. Poulsen and Iversen (2008) concluded that the paradigm of the copepod “coprophagous filter” of González and Smetacek (1994) that removes fecal pellets from the epipelagic water column should perhaps be changed to a “protozoan filter.”

The importance of dinoflagellates in degradation of copepod fecal pellets was further confirmed from the studies of Poulsen et al. (2011). Feeding on *Acartia tonsa* fecal pellets by 4

heterotrophic and 3 mixotrophic dinoflagellate species was investigated through a combination of feeding and dinoflagellate growth experiments and video recordings of feeding behavior. Two of 3 mixotrophic and all 4 heterotrophic dinoflagellates fed upon fecal pellets and grew upon diets of fecal pellets. Feeding upon fecal pellets involved different types of dinoflagellate behavior, including direct engulfment of entire fecal pellets, removal of only small pieces of fecal pellets for ingestion, attachment of a peduncle (feeding tube), stretching of the dinoflagellate cell membrane around a fecal pellet to bend and fold the pellet into a food vacuole, and pallium (feeding veil) feeding outside the dinoflagellate theca.

Using natural concentrations of dinoflagellates and copepod fecal pellets, and measured ingestion rates, Poulsen et al. (2011) calculated that large (>20 µm in size) dinoflagellates alone can account for reported rates of fecal pellet degradation in field studies, confirming the importance of dinoflagellates in the protozoan filter for sinking fecal pellets. Thus, the study of Poulsen et al. (2011) expanded upon previous observations (Kørboe, 2003) of ingestion of copepod fecal pellets by the heterotrophic dinoflagellate *Noctiluca scintillans*, and suggested that dinoflagellate coprophagy is more widespread than previously realized.

Svensen et al. (2012) further examined the degradation of copepod fecal pellets by protozooplankton. Degradation of large (590 + 97 µm length) fecal pellets produced by the copepod *Calanus finmarchicus* was examined during incubations of natural seawater (<180 µm), which contained natural assemblages of plankton. The plankton assemblages were dominated by athecate dinoflagellates and ciliates. Degradation of fecal pellets was time-dependent with no degradation apparent after 20 or 48 h, but with reduction of fecal pellet volume by 32% after 72 h. Large copepods helped to facilitate the degradation process, in that degradation increased to 75% of fecal pellet volume after only 48 h in containers that had *C. finmarchicus* in addition to <180 µm natural plankton assemblages. Svensen et al. (2012) concluded that ciliates and dinoflagellates could degrade the large copepod fecal pellets, but that the process was too slow to explain observed retention of these large fast-sinking fecal pellets in the upper 200 m of the water column. Svensen et al. (2012) suggested that combined effects such as microbial degradation, and coprophagy or coprophagy by copepods and protozooplankton, of different-sized fecal pellets over relevant time frames were more likely than single-factor explanations to explain the retention of fecal pellets in epipelagic waters.

Not all zooplankton fecal material is in the form of fecal pellets. Olesen et al. (2005) found that over half of the fecal matter released by the copepod *Acartia tonsa* in Danish coastal waters was in the form of small (<10 µm), slowly-sinking particles that were not surrounded by a peritrophic membrane. These tiny particles sank slowly (5 m d⁻¹), but degraded rapidly (approximately 50% d⁻¹). Olesen et al. (2005) concluded that when the non-pellet-bound fecal material was included, that 80% of the copepod fecal matter would be recycled within the upper 15 m of the water column.

Zooplankton vertical migration and fecal pellet repackaging

In addition to grazing on phytoplankton and producing sinking fecal pellets that contribute to the vertical export flux to depth, zooplankton can also actively export organic material to depth through their own vertical migration. In the “active flux” by vertically-migrating zooplankton (reviewed by Packard and Gómez (2013)), food ingested near the surface is carried downward in the guts of migrating zooplankton to be egested, eaten by consumers of zooplankton, or otherwise metabolized at depth. Estimates of the downward transport of carbon through active flux (from studies published prior to early 2001) usually averaged only

4–34% of the sinking POC, but could approach 70% (see references in Ducklow et al., 2001; Steinberg et al., 2002; Turner, 2002). Ducklow et al. (2009) estimated that the annual export flux due to vertical migrators was 10–20% of the sinking particle flux in the North Pacific (HOT) and North Atlantic (BATS) subtropical gyres, but this active flux could equal the sinking particle flux during times of high zooplankton biomass. Yamaguchi et al. (2002) estimated that suspension-feeding and detritivorous copepods consumed an average of 32% of the POC flux in the upper 4000 m of the water column in the western subarctic Pacific. Many of these copepods were vertical migrators, and calculations suggested that there were sufficient suspension-feeding and detritivorous copepods to meet the metabolic needs of carnivorous copepods. Thus, the copepod community likely contributed to the active export flux to depth. Bollens et al. (2011) noted that a variety of field studies from most of the world's oceans indicated that diel vertical migration by zooplankton accounts for 10–50% of the total vertical flux of carbon and nitrogen downward from epipelagic layers.

The importance of zooplankton migrant active flux appears to vary with hydrographic and biological conditions. Hernández-León et al. (2001) estimated that migrant active flux was 3–25% of estimated particle export flux in waters of the Canary Islands. However, in anticyclonic eddies zooplankton migrant biomass was double that of surrounding waters, and active flux of POC by vertical migrants could be as high as 53% of passive carbon flux to the mesopelagic zone (Yebra et al., 2005). Conversely, Putzeys et al. (2011) estimated that the total carbon flux to 200 m due to diel vertical migrants was only 3–9% of the POC flux at the end of the late winter bloom off the Canary Islands. Schnetzer and Steinberg (2002) estimated that active flux of POC averaged 3%, with a maximum of 18% of mean gravitational sinking flux measured by sediment traps at 150 m. Schnetzer and Steinberg (2002) also noted that feces that were freshly-defecated at depth by migrants could be more valuable food for mesopelagic consumers than feces produced in epipelagic waters that had been decomposing while sinking to depth.

The downward flux of carbon due to vertically-migrating zooplankton sometimes approaches or exceeds the flux of carbon from sinking fecal pellets and other particulates. At two sites in the subarctic and subtropical northwestern North Pacific, the estimated downward flux of carbon due to vertically-migrating zooplankton during winter was greater (131–136%) than the flux of sinking fecal pellets (Kobari et al., 2013). Takahashi et al. (2009) estimated that annual carbon transport by diel vertical migration of two species of the copepod genus *Metridia* was 15% of the annual total flux of POC to 150 m depth in the subarctic North Pacific Ocean. Since diel vertical migration by these copepods was more active during the non-spring-bloom season, when sedimenting flux of phytoplankton and other particulate organic matter was low, *Metridia* spp. were important in driving the biological pump in the subarctic Pacific during seasons other than spring. Stukel et al. (2013a) estimated that active transport of carbon by migratory zooplankton was 1.9–40.5% of the passive sinking flux to 100 m depth in the California Current Ecosystem.

Steinberg et al. (2008a) estimated the losses of POC in the mesopelagic zone due to bacterial versus zooplankton metabolism in both the subtropical Pacific and subarctic Pacific. Estimates suggested that sinking POC was insufficient to meet metabolic demands of either the zooplankton or the bacteria at either site. Steinberg et al. (2008a) concluded that the additional mesopelagic carbon demands must have been met by active flux from vertical migration of the zooplankton from the epipelagic to the mesopelagic zones. Hernández-León et al. (2010) found that the estimated active flux to the mesopelagic off the Canary Islands peaked each month at the time of the full moon, and suggested that this pulse was similar to that of the gravitational particle flux, and that this

might explain some of the discrepancy noted by Steinberg et al. (2008a). Lunar cycles were also apparent in the vertical migration patterns recorded by Ochoa et al. (2013) in the Gulf of Mexico. A model in which migration velocities were different at different depths, and particulate organics were recycled at different depths led Ochoa et al. (2013) to propose that sequential vertical migrations at different depths transported POC to depth like a "bucket brigade."

At the same two sites in the North Pacific studied by Steinberg et al. (2008a), Wilson et al. (2008) found evidence of repackaging of sinking fecal pellets and zooplankton carnivory in the mesopelagic. Changes in flux, size, shape, and color of zooplankton fecal pellets with depth suggested that many sinking fecal pellets were fragmented by other zooplankton, with subsequent re-ingestion of fecal pellet contents.

Kobari et al. (2008) estimated that fecal pellet flux by the copepod community in the subarctic North Pacific was 141–223% of the sedimenting POC flux to 150 m. This suggested that there was repackaging of fecal pellets in the epipelagic, and that copepod-fecal-pellet active transport to depth was important in the carbon flux to depth, particularly during seasons when the phytoplankton was dominated by small cells that would not be expected to sink rapidly. Additionally, Kobari et al. (2003) estimated that carbon flux due to mortality of copepods overwintering at depth was equal to or greater than the sedimenting flux in the subarctic North Pacific.

Consumption of particulate matter originating in the epipelagic by mesopelagic zooplankton has been indicated by two different techniques. Wilson et al. (2010) used fatty acid biomarkers to characterize zooplankton diets and particle composition in waters in the mesopelagic down to 1000 m in the subarctic and subtropical North Pacific. Proportions of fatty acid biomarkers in both zooplankton and particulate assemblages were similar, indicating that zooplankton were consuming sinking particles. Markers indicative of carnivory by mesopelagic zooplankton increased with depth. Wilson and Steinberg (2010) analyzed gut contents of mesopelagic copepods and ostracods down to depths of 1000 m using light and epifluorescence microscopy, and found that cyanobacteria and eukaryotic phytoplankton too small to have been ingested individually were present in guts. This indicated that zooplankton feeding on detrital aggregates with attached picoplankton was a pathway for enhanced transport of surface primary production to depth. However, Hannides et al. (2013) concluded from studies using stable isotopes of nitrogen and carbon that mesopelagic zooplankton in the subtropical North Pacific utilized mainly surface-derived rather than mesopelagic suspended food resources, through consumption of sinking particles, carnivory of vertical migrants, or epipelagic feeding by vertical migrants at night.

Zooplankton vertical migration can also be important in the flux of DOM to depth. Steinberg et al. (2002) found that excretion of dissolved organic nitrogen by migrating zooplankton was 15–66% of total dissolved nitrogen excreted by the total zooplankton community in the Sargasso Sea. Active transport of total dissolved nitrogen averaged 13%, 18%, and 27% of the mean monthly sinking flux of particulate organic nitrogen to depths of 150, 200, and 300 m, respectively. Maximum flux of total dissolved nitrogen from migrators was 1.6–3.5 times greater than the sinking particulate organic nitrogen flux at these three depths.

Active export by vertically-migrating zooplankton can be important in the removal of phosphorus from the surface ocean. Hannides et al. (2009) found that migrant-mediated fluxes of phosphorus averaged 82% of phosphorus fluxes to sediment traps at 150 m, 300 m and 500 m in the North Pacific Subtropical Gyre. Since migrant zooplankton biomass and thus the importance of this mechanism for removal of phosphorus from epipelagic waters had increased over the period from 1994 through 2005, active flux

may be a major driving force for enhanced phosphorus limitation of primary production in this area.

Microbial ecology of fecal pellets

Zooplankton fecal pellets and other organic particulate matter such as marine snow and phytoplankton aggregates are “microbial hotspots” in the sea. Fecal pellets and other detrital particles harbor dense populations of bacteria and other microbes at abundance levels that are orders-of-magnitude higher than in the surrounding water (Azam and Long, 2001; Simon et al., 2002). These microbes decompose as well as colonize and grow upon the particles with which they are associated. Microbial colonization can enhance the nutritional quality of fecal pellets and other organic aggregates for detritivorous consumers (Grossart et al., 2003a, 2003b). Sinking aggregates also release dissolved solutes to the surrounding water column (Kiørboe et al., 2001; Ploug, 2001; Ploug et al., 2002).

Colonization of organic aggregates by bacteria is constantly changing as motile bacteria and other microbes both attach to, and detach from particles. There is a succession of trophic interactions within the community of microbes attached to particles, in which bacterial abundances are controlled by flagellate predation, and flagellate and ciliate populations turn over rapidly due to ongoing attachment and detachment (Artolozaga et al., 2002; Kiørboe, 2003, 2004; Kiørboe et al., 2002, 2003, 2004; Grossart et al., 2003b). Grossart and Ploug (2001) found that decomposition of particulate organic matter by attached microbes was substantial, and that the vertical flux of particles in the ocean was greatly reduced during sinking. Most of the bacteria attached to particles exported to depth in arctic waters appeared to have come from near-surface suspended bacteria that attached to sinking particles (Tamelander, 2013).

In addition to bacteria attached to particles, there are bacteria inside fecal pellets of copepods (Tang, 2005; Tang et al., 2001; Thor et al., 2003; Jing et al., 2012; Köster et al., 2011) and doliolids (Köster et al., 2011). Tang (2005) noted that copepods introduce organic substrates into their guts and fecal pellets through ingestion of food, and that bacteria use these organic substrates for rapid growth. Bacterial abundance increased in copepod guts with increasing ingestion rates (Tang, 2005). Thus, there is a balance between bacterial growth stimulated by copepod feeding and bacteria loss through copepod defecation. Tang (2005) also found that the bacterial abundance associated with copepods and their fecal pellets was orders-of-magnitude higher than for free-living bacterioplankton in surrounding waters.

Release of DOM from degrading aggregates and fecal pellets provides substrate for growth of bacterioplankton in the surrounding water that are not attached to particles. Copepod fecal pellets have been shown to release DOC during degradation (Møller et al., 2003; Thor et al., 2003; Saba et al., 2011), although fecal pellets of salps did not release measurable chromophoric (or colored) DOM (Steinberg et al., 2004). Møller et al. (2003) found that leakage of DOC from newly-expelled fecal pellets of *Calanus finmarchicus* can be as high as 28% within 15 min. Saba et al. (2011) found that fecal pellets of the copepod *Acartia tonsa* also released ammonium and urea. Itoh et al. (2007) found that loss of organic matter from fecal pellets of epifaunal grazers of *Sargassum* was rapid, presumably due mainly to loss of DOM.

Rates of microbial degradation of zooplankton fecal pellets and other types of organic aggregates influence the extent to which these particles are recycled near-surface or exported to depth. There is little available information on microbial degradation rates of fecal pellets or other organic particles in the sea. Thor et al. (2003) found that rates of decomposition of copepod fecal pellets varied depending on the diets used to produce the pellets. Fecal pellets of *Acartia tonsa* decomposed at rates of 9, 14, and 19% d⁻¹

for diatom-, cryptophyte-, and dinoflagellate-based pellets, respectively. Olesen et al. (2005) found rates of degradation of *A. tonsa* fecal pellets of <5% d⁻¹ at 16–17 °C. Ploug et al. (2008a) found rates of microbial degradation of fecal pellets from *Temora longicornis* at 15 °C of 8–16% d⁻¹. Köster and Paffenhofer (2013) found that doliolid fecal pellets lost 2% of the total organic carbon within the first 4 h of pellet degradation at 21.9 °C.

Olsen et al. (2005) developed an isothermal microcalorimetry technique to quantify microbial degradation of copepod fecal pellets at 18 °C. Fecal pellet degradation rates using this technique were dependent upon pellet carbon:volume ratios, which previous literature showed could have order-of-magnitude variations from 0.02–0.39 pg C µm⁻³ (references in Olsen et al., 2005). Thus, using the highest ratio (0.39 pg C µm⁻³), degradation was 28 + 18% of fecal pellet carbon within the first 20 h. For a ratio of 0.25 pg C µm⁻³, degradation was 45 + 27% of fecal pellet carbon within the first 20 h. For a ratio of 0.085 pg C µm⁻³, degradation was >100% of fecal pellet carbon within the first 20 h. Olsen et al. (2005) did not measure the carbon:volume ratios of fecal pellets in their experiments, but noted that this should be done in future studies since this ratio varies greatly with type of food used to produce the fecal pellets. Further, results of Olsen et al. (2005) suggested that copepod fecal pellets contained anaerobic bacteria, indicative of anoxic microbial activity within the fecal pellets. The presence of methanogenic Archaea within copepod fecal pellets, indicating such anoxic micro-sites, was recently confirmed by Ditchfield et al. (2012). Also, Tang et al. (2011) recently confirmed that metosome portions of the guts of calanoid copepods were acidic and suboxic to anoxic, relative to seawater. Thus, copepod guts and fecal pellets may be microhabitats for strict anaerobes in an otherwise oxygenated water column.

There have long been questions as to the comparative importance of bacteria contained within fecal pellets prior to egestion versus bacteria from the surrounding water that colonize fecal pellets after egestion, and whether bacterial degradation of zooplankton fecal pellets is primarily from the “inside out” or the “outside in” (references to papers published before 2001 in Turner, 2002). Recent studies by Jing et al. (2012) and Cnudde et al. (2013) reveal that both processes occur. Jing et al. (2012) examined the bacterial communities associated with fecal pellets from a mixture of copepods from coastal waters of Hong Kong. The fecal pellets contained bacteria that were composed of different phylogenetic groups from those living in the natural seawater. Bacterial communities in seawater had higher species richness than those in fecal pellets. There were major shifts in the bacterial community composition associated with fecal pellets in the first two days of experimental incubations in natural seawater. Bacteria that were initially found to be only associated with fecal pellets were never found in surrounding seawater, but the communities of bacteria in fecal pellets and seawater became more similar with time, indicating that bacteria from surrounding seawater colonized fecal pellets during experimental degradation incubations. Jing et al. (2012) suggested that colonization of fecal pellets by bacteria from surrounding seawater was an important part of the pellet decomposition process. Similarly, Cnudde et al. (2013) found that dissolved organic matter from copepod fecal pellets was consumed by free-living bacterioplankton, whereas particulate matter was degraded by internal bacteria within fecal pellets, or external bacteria attached to the surfaces of fecal pellets. Internal and external bacteria associated with fecal pellets and bacterioplankton all had different phylotypes based on molecular analyses. Cnudde et al. (2013) concluded that degradation of copepod fecal pellets by internal bacteria was as important as degradation by bacteria that colonized fecal pellets from the surrounding water. De Troch et al. (2010) found that the bacteria associated with a marine harpacticoid copepod and its fecal pellets mainly originated from the copepod's gut, and that the composition

of bacterial communities of the copepods' guts depended on the initial food sources ingested by the copepods.

Decomposition of copepod fecal pellets might consume substantial amounts of oxygen in some situations. Shek and Liu (2010) calculated that decomposing copepod fecal pellets in the warm (28 °C) waters of Hong Kong in summer might consume 30–45% of saturation dissolved oxygen concentration, possibly contributing to bottom-water anoxia.

Some fast-sinking particles such as fecal pellets and marine snow appear able to fall through the water column with minimal microbial degradation due to the effects of pressure. Tamburini et al. (2009) showed that particles (mostly fecal pellets) collected from the Mediterranean at 200 m depth were less degraded by prokaryotes under increasing pressure, simulating descent from 200 m to 1500 m. A decrease in the abundance of prokaryotes attached to particles, as well as chemical evidence, suggested that degradation of fecal pellets was reduced by increasing pressure as these particles sank through the mesopelagic zone. In the experiments of Tamburini et al. (2009), the same microbial population was exposed to different levels of pressure, whereas in the sea, the composition of microbial communities changes with depth as pressure changes.

Sinking velocity of fecal pellets and aggregates, and ballasting by mineral contents

Sinking velocities of fecal pellets and aggregates are highly-variable, and may be affected by comparatively-dense mineral ballast such as phytoplankton thecae or terrigenous particles. Turner (2002) reviewed measurements of fecal pellet sinking velocity from publications up through a portion of 2001. Sinking velocities for copepod and appendicularian fecal pellets were up to 220 m d⁻¹, whereas those for fecal pellets of larger animals were faster (up to 862 m d⁻¹ for fecal pellets from euphausiids, 504 m d⁻¹ for fecal pellets from doliolids, 2700 m d⁻¹ for fecal pellets from salps, 646 and 1800 m d⁻¹ for fecal pellets from heteropods and pteropods, and 1313 m d⁻¹ for fecal pellets from chaetognaths).

Subsequent studies have extended some of these ranges, and shown that ballasting fecal pellets and aggregates such as marine snow or phytoplankton detritus with comparatively-dense hard contents such as diatom tests and coccoliths may increase pellet sinking velocity (Armstrong et al., 2002; François et al., 2002; Klaas and Archer, 2002). "Ballast" biominerals in phytoplankton such as opal (SiO_2) and coccoliths (CaCO_3), or lithogenic materials such as wind-blown dust, have been proposed to increase the density and sinking flux of fecal pellets and other particles that contain these minerals (De la Rocha et al., 2008; Poulton et al., 2006; Sanders et al., 2010; Thomalla et al., 2008). Organic carbon export fluxes have been correlated with mineral fluxes, particularly for carbonate, but less so for opal and terrigenous materials (Armstrong et al., 2002; François et al., 2002; Klaas and Archer, 2002). These ballast minerals have been suggested to also protect some of the organic matter in particles from being microbially biodegraded in the deep ocean (Armstrong et al., 2002, 2009; François et al., 2002; Klaas and Archer, 2002). Thus, the diets of zooplankton may strongly affect the sinking velocities of their fecal pellets, depending on the types and concentrations of ballast minerals ingested.

The ballast hypothesis was examined experimentally by Ploug et al. (2008a, 2008b). Ploug et al. (2008a) measured rates of fecal pellet production and microbial respiration, and sinking velocity for fecal pellets of the copepod *Temora longicornis* fed upon diets of three types of phytoplankton: the nanoflagellate *Rhodomonas* sp., which contained only organic carbon, the diatom *Thalassiosira weissflogii*, which contained opal, and the coccolithophorid *Emilia nia huxleyi*, which contained calcite. Due to higher densities from ballasting by opal and calcite, sinking velocities for fecal pellets

produced on diets of the diatom ($322 \pm 169 \text{ m d}^{-1}$) and the coccolithophorid ($200 \pm 93 \text{ m d}^{-1}$) were significantly higher than for pellets produced on a diet of the microflagellate ($35 \pm 29 \text{ m d}^{-1}$). However, rates of microbial respiration (0.15 d^{-1}) were not significantly different on the three different diets. Ploug et al. (2008a) concluded that ballast increased the sinking velocity of copepod fecal pellets but did not protect pellets from decomposition. Similarly, Iversen and Ploug (2010) found that carbonate-ballasted coccolithophorid aggregates of marine snow sank faster than opal-ballasted diatom aggregates, but that there was no difference in carbon-specific respiration rates for aggregates with different ballast. Ploug et al. (2008b) measured dry mass, sinking velocity and diffusivity of natural fecal pellets collected from sediment traps off Cape Blanc, Mauritania. Large fecal pellets were heavily ballasted with opal, calcite, and Saharan dust. Average sinking velocities of these pellets were $51\text{--}732 \text{ m d}^{-1}$. Thus, natural ballast increased the sinking velocities of fecal pellets.

Patonai et al. (2011) measured sinking velocities of fecal pellets from the doliolid *Dolioletta gegenbauri*, and recorded velocities ($25\text{--}68 \text{ m d}^{-1}$), which were much slower than previous measurements for the same species. The differences in sinking velocities were attributed to differences in the diets used to produce the fecal pellets, with non-ballasted diets producing fluffy slowly-sinking fecal pellets. In another study with fecal pellets from planktonic tunicates, sinking velocities of fecal pellets from unspecified salps in the Arabian Sea were high, with a range of $400\text{--}900 \text{ m d}^{-1}$ (Ramaswamy et al., 2005).

Not all examinations of the "ballast hypothesis" have supported it. Berelson (2002) found that sinking velocities of particles collected by sediment traps in the Arabian Sea and Equatorial Pacific increased with depth. This increase was correlated with loss of organic carbon with depth, but not with lithogenic mineral content. Due to the increases in sinking velocities with depth, Berelson (2002) concluded that lithogenic contents of particles did not impact settling rates. Hamm (2002) found that addition of lithogenic mineral particles to diatom aggregates had ambiguous effects on aggregate sinking velocities. Increasing amounts of lithogenic material increased aggregate sinking rates until aggregates became saturated, and further increases in lithogenic material either caused no significant increases in sinking velocities of aggregates, or even decreased sinking velocities. Passow and De La Rocha (2006) found that incorporation of minerals into aggregates reduced the size of aggregates and their sinking velocities. Lombard et al. (2013b) found that ballasting with calcite (coccoliths) and Saharan dust increased the sinking velocities of marine snow from discarded appendicularian houses, but that opal (diatoms) had only a minor effect.

Passow (2004) argued that rather than mineral ballast determining POC fluxes to depth, POC fluxes determine fluxes of mineral ballast materials. The reason was that sinking marine snow originating from surface-layer biological processes may collect small, non-sinking mineral particles and transport them to depth. Passow and De La Rocha (2006) found that sinking velocities of phytodetritus aggregates with various amounts of mineral ballast were not straightforward, and that the flux of POC determined the flux of minerals to depth, and not the other way around.

There have been several recent measurements of zooplankton fecal pellet sinking velocity which suggest that water temperature also affects pellet sinking velocity. Giesecke et al. (2010) found that fecal pellets from the Antarctic chaetognath *Sagitta gazellae* sank at speeds of $33\text{--}600 \text{ m d}^{-1}$, averaging 243 m d^{-1} . Pellets from *S. gazellae* were large ($2\text{--}10 \text{ mm}^3$), and their sinking velocities increased with pellet volumes. A comparison of pellet volumes and sinking velocities with previously-published data suggested that fecal pellets of *S. gazellae* were among the fastest-sinking fecal pellets that have yet been measured. However, sinking velocities of *S. gazellae*

were lower than those recorded for other chaetognaths by Dilling and Alldredge (1993). Giesecke et al. (2010) attributed this difference to that of temperature of the water used in the sinking velocity experiments. Dilling and Alldredge (1993) used water at approximately 20 °C for their measurements, whereas Giesecke et al. (2010) used water at 0 °C. The importance of water temperature for fecal pellet sinking velocities also emerged from measurements by Bach et al. (2012a, 2012b) of sinking velocities of fecal pellets of unknown origin collected by sediment traps. Bach et al. (2012a, 2012b) found that an increase of 9 °C led to increases in sinking velocity of 40%.

The sinking velocities of fecal pellets from Antarctic euphausiids (*Euphausia superba*) vary greatly with diet and food absorption (Atkinson et al., 2012). Fecal pellets from over 40 euphausiid schools sampled in spring, summer and fall in the Scotia Sea sank at velocities of 27–1218 m d⁻¹ (median 304 m d⁻¹). Pellet sinking velocities were related mainly to pellet diameter (80–600 µm) and density. Pellet density was related to feeding rates and food assimilation. When feeding rates were low, slow gut passage times and high food absorption efficiency resulted in pellets that were compact, dense, low in carbon and nitrogen content and fast-sinking. Conversely, when feeding conditions were good, pellets had fast gut passage times and inefficient food absorption, producing pellets that had high carbon and nitrogen contents, and sank slowly. Food composition was also important in that diatom diets produced fast-sinking pellets that were likely ballasted by silicon. Fecal pellets produced on non-diatom phytoplankton diets sank more slowly. Thus, depending on how euphausiids processed their food, fecal pellets could be either fast-sinking promoting organic matter export to depth, or slow-sinking but high in carbon and nitrogen, providing food for water-column detritivores. Even though euphausiid fecal pellets generally sank more slowly than those of salps (up to 1640 m d⁻¹ – Pakhomov et al., 2006; Phillips et al., 2009), euphausiid fecal pellets were more frequently dominant in samples from sediment traps in the Antarctic. Atkinson et al. (2012) suggested that this was because euphausiid schools are more compact, producing showers of fecal pellets that exceed the capacity of pelagic scavengers to eat them.

Røstad and Kaartvedt (2013) used an upward-facing echo sounder to measure sinking velocities of fecal pellets of the euphausiid *Meganyctiphanes norvegica* in Oslofjord, Norway. Recorded sinking velocities were 423–804 m d⁻¹, with highest sinking velocities during the spring diatom bloom in March.

Temperature also affects sinking velocities of aggregates other than fecal pellets. Iversen and Ploug (2013) examined formation, degradation, and sinking velocity of laboratory-produced diatom aggregates at 15 °C and 4 °C. Respiration rates at 15 °C were reduced 3.5-fold at 4 °C. Although no direct influence of temperature on aggregate sinking velocity was recorded, Iversen and Ploug (2013) concluded that temperature was important for vertical fluxes of POC due to cold temperatures slowing the degradation of aggregates by incorporated warm-temperature epipelagic microbes.

Phytoplankton cysts, intact cells and harmful algae toxins in fecal pellets and sediment traps

When zooplankton feed upon toxic or otherwise harmful species of phytoplankton, zooplankton fecal pellets may provide a mechanism by which cysts, intact cells, and/or toxins from harmful algae are transported from pelagic to benthic environments, thereby potentially contaminating suspension-feeding bivalves or other shellfish. Zooplankton fecal pellets have been shown to contain cysts or intact cells of harmful algae species. Resting cysts of toxic dinoflagellates that were capable of subsequent germination have been found in the fecal pellets of copepods and some benthic

organisms (Persson, 2000; Persson et al., 2006; Tsujino et al., 2002, and references therein). Intact cells of dinoflagellates of the toxin-producing genus *Dinophysis* were in fecal pellets of copepods grazing upon natural *Dinophysis* blooms in the North Sea (Wexel Riser et al., 2003) and off Spain (Maneiro et al., 2002). These fecal pellets were suggested to be a potential source of toxins to pelagic components of the food web, through coprophagy, or to the benthos through fecal pellet sedimentation. Dinoflagellate resting cysts (Montresor et al., 2003), and vegetative cells of certain dinoflagellate and diatom species (Jansen and Bathmann, 2007) survived ingestion by copepods and remained viable in copepod fecal pellets.

Phycotoxins can also occur in fecal pellets of grazers feeding on diets of toxic algae. Fecal pellets from copepods contained toxins from cyanobacteria (Lehtiniemi et al., 2002) and dinoflagellates (Teegarden et al., 2003). Also, Petitpas et al. (2014) confirmed dinoflagellate toxins in fecal pellets from zooplankton assemblages that were dominated by the marine cladoceran *Evadne nordmanni* during natural blooms of the toxic dinoflagellate *Alexandrium fundyense* in the Gulf of Maine. Svensen et al. (2005) found that when the mussel *Mytilus edulis* fed upon the toxic cyanobacterium *Nodularia spumigena*, mussel fecal pellets retained cyanobacterium toxins, but when these toxic feces were fed to other mussels, coprophagy reduced toxins in feces by 99%. Whether the same applies to coprophagy by zooplankton is unknown. Also, Rosa et al. (2013) found that feces from several species of biofouling benthic ascidians contained viable cells of several species of toxic harmful phytoplankton.

During some harmful algal blooms, toxic phytoplankton can sink directly to depth. Sekula-Wood et al. (2009, 2011) found cells of the toxic diatom *Pseudo-nitzschia* spp. and the phycotoxin domoic acid from diatoms of this genus in sediment traps from off California during blooms of this diatom. A 15-year time-series of these samples revealed an abrupt increase with more frequent and abundant *Pseudo-nitzschia* blooms and toxic domoic acid events after the year 2000, possibly related to climate variability due to the North Pacific Gyre Oscillation.

Importance of fecal pellets from various types of zooplankton

Fecal pellets from a variety of zooplankters contribute to the biological pump. There have been several studies of the importance of fecal pellets produced by various zooplankters that have been published since the review of Turner (2002). Included are studies of fecal pellets of salps, appendicularians, pteropods, chaetognaths, copepods, euphausiids, and heterotrophic dinoflagellates. Most of these measurements were for fecal pellets sinking through settling columns aboard ship or in the laboratory.

Salp fecal pellets can be major components of vertical flux during salp swarms in the Arabian Sea (Ramaswamy et al., 2005), in slope water off the northeastern United States (*Salpa aspera* – Madin et al., 2006), and in the Southern Ocean (*Salpa thompsoni* – Pakhomov et al., 2006; Phillips et al., 2009).

Both simulations (Berline et al., 2011) and sediment-trap collections (Wilson et al., 2013) indicate that appendicularian fecal pellets are an important component of the export flux to depth. Appendicularians filter small-sized phytoplankton cells and repackage them into larger fecal pellets (Deibel and Turner, 1985), which sink to depth. Appendicularian fecal pellets dominated the flux after a change of water mass due to advection of warm Atlantic water into Fram Strait east of Greenland (Lalande et al., 2011). Appendicularians (*Oikopleura dioica* and *Fritillaria borealis*) were also important contributors to the vertical flux (fecal pellets and houses) in a Swedish fjord in the fall when *O. dioica* was abundant, but not in the spring when *F. borealis* was abundant (Vargas et al., 2002). In the North Water polynya of Baffin Bay, fecal

pellets from the appendicularian *Oikopleura vanhoeffeni* accounted for 4% of the median daily carbon export from the euphotic zone (Acuña et al., 2002).

Fecal pellets of pteropods and chaetognaths can be important components of the export flux in the Antarctic. Fecal pellets of the pteropod *Limacina helicina* contributed 10–30% (mean = 19%) of the total POC flux to 180 m over 4 years (1998–2001) in Terra Nova Bay, Ross Sea, Antarctica (Manno et al., 2010). Fecal pellets from the chaetognath *Sagitta gazellae* contributed 12% of the total vertical carbon flux to 360 m depth in winter (ice-covered) and 5% in summer (ice-free) in the Lazarev Sea of the Southern Ocean (Giesecke et al., 2010).

The contribution of copepod fecal pellets to vertical export is variable, and size-dependent. Møller et al. (2011) found that the export of fecal pellets from small copepods (copepods <200–400 µm in length) to depths below 400 m was negligible in the southern Indian Ocean, and >99% of these fecal pellets were recycled in the upper 400 m. Conversely, Dagg et al. (2003) found that the export of POC from large copepods (late stage copepodites or adult females of *Rhincalanus gigas*, *Calanoides acutus*, *Calanus simillimus*, *Calanus propinquus*, *Neocalanus tonsus*, *Pleuromamma robusta*, *Metridia* spp.) to 100 m depth in the Antarctic Polar Front (170°W) was more substantial. Copepod fecal pellet production was 22–63% of the POC flux in spring, but only 2–7% in summer. Dagg et al. (2003) estimated that most of these fecal pellets were recycled in the upper 1000 m of the water column.

Gleiber et al. (2012) examined the relative contributions of fecal pellets of euphausiids, copepods and salps in the POC flux to 170 m depth off the western Antarctic Peninsula. Fecal pellet POC was the dominant component of total organic carbon flux with significantly higher pellet flux (67%) in summer (November to April) than in winter (May to October) (34%). Cylindrical euphausiid fecal pellets contributed a monthly mean of 72% of the total fecal pellet flux, with ovoid copepod and tabular “flake” salp fecal pellets contributing significantly less (22% and 6%, respectively). Export of cylindrical and ovoid fecal pellets, presumably from euphausiids and copepods, was significantly higher in summer, whereas 48% of tabular fecal pellet flux (presumably from salps) occurred in winter. Euphausiid fecal pellets were the dominant component of the fecal pellet export flux off the western Antarctic Peninsula. Antarctic krill depend on high phytoplankton food availability in summer, and sea ice habitat for larval recruitment in winter, whereas salps can survive in open waters of lower phytoplankton abundance, and do not require sea ice as a habitat (Atkinson et al., 2004; Quetin and Ross, 2001). Thus, recent declines in sea ice habitat, chlorophyll, and the abundance of euphausiids compared to salps due to climate change may also impact the export of particulate organic matter to depth off the western Antarctic Peninsula.

Lam and Bishop (2007) also found indications of the importance of euphausiids in the export flux in austral summer in the Southern Ocean. Mesopelagic waters (100–1000 m depth) in the Antarctic at 66°S had a steeper decline in amounts of POC with depth than in the Subantarctic at 55°S. This was despite the order-of-magnitude higher levels of >51 µm-sized POC in diatom-dominated surface waters at 66°S than in coccolithophorid-dominated surface waters at 55°S. The differences were apparently due to intensive zooplankton grazing in the upper 150 m, as evidenced by abundant large (several mm long) fecal pellets at 66°S, most likely produced by euphausiids. Below 200 m depth, there was an almost complete removal of large phytoplankton aggregates, presumably by zooplankton grazing.

Heterotrophic dinoflagellates also produce fecal pellets that contain remains of ingested diatoms (Buck et al., 2005, and references therein). A large (100 µm long, 50 µm wide) teardrop-shaped aethocyst dinoflagellate of the genus *Gyrodinium* ingested a variety of diatom species in Monterey Bay, California. However,

Buck et al. (2005) suggested that these dinoflagellates were rarely abundant and had a minor role in feeding on diatoms in Monterey Bay, even though fecal pellets from these dinoflagellates were occasionally abundant in the water column.

Fecal pellets from radiolarians appear to be important exporters of organic carbon to the deep ocean (Lampitt et al., 2009). Large episodic pulses of organic matter have repeatedly been shown to sink to 3000 m in late summer and early fall in the northeast Atlantic. Radiolarians have been independently (Continuous Plankton Recorder survey) shown to be abundant in this area in late summer/early fall, and interannual variability in radiolarian abundance closely mirrored the interannual variability in deposition of organic matter to the deep sea in this region. Material collected in sediment traps showed strong correlation between radiolarian fecal pellets and organic carbon flux. Lampitt et al. (2009) concluded that radiolarian fecal pellets were responsible for the pulses of organic matter deposition in the northeast Atlantic in late summer/early fall.

Zooplankton fecal pellets can also concentrate pollutants. Lee et al. (2012) showed that the doliolid *Dolioletta gegenbauri* ingested oil droplets produced by treating crude oil with dispersants as in an oil spill, and that resulting fecal pellets contained abundant oil droplets. Lee et al. (2012) concluded that doliolid ingestion of oil droplets and production of oil-laden fecal pellets could be a significant mechanism by which oil is delivered to the benthos during a spill.

Zooplankton fecal pellets and picoplankton export

Zooplankton fecal pellets can provide a mechanism for the export of photosynthetic picoplankton from the euphotic zone to depth. Picoplankton cells (<2 µm in size) are major components of the ocean's phytoplankton biomass and productivity. These tiny cells are generally thought to be too small to sink as individual cells, or to be efficiently grazed by larger mesozooplankton (>200 µm in size). Thus, picoplankton generally have been thought to contribute little to export flux, unless these cells become attached to sinking aggregates, marine snow or phytodetritus.

The view of picoplankton in export flux is changing, due to recent evidence of substantial incorporation of picoplankton into sinking fecal pellets. There are recent observations of intact and/or degraded picoplankton cells in the mesopelagic water column (Lomas and Moran, 2011) and in sediment traps (Amacher et al., 2009, 2013; Lamborg et al., 2008), using flow cytometry, microscopy, and molecular or diagnostic pigment techniques. Modeling studies of Richardson and Jackson (2007) also suggest that picoplankton contribute substantially to export flux.

Stukel et al. (2013b) confirmed that the picoplanktonic cyanobacterium *Synechococcus* was exported to depth in zooplankton fecal pellets in the Costa Rica upwelling dome. Although *Synechococcus* was a dominant component of the total phytoplankton production, flow cytometry measurements of material from sediment traps at the base of the euphotic zone revealed that ungrazed *Synechococcus* contributed only 0.11% of the carbon export. However, levels of phycoerythrin (a cyanobacteria marker pigment) in the same samples from sediment traps revealed that intact unassimilated *Synechococcus* cells in fecal pellets gave eight-times higher export contributions than ungrazed sinking cells.

Grazing of mesozooplankton on *Synechococcus* cells was confirmed by levels of phycoerythrin in zooplankton guts, as well as visual observations of *Synechococcus* cells in fecal pellets (Stukel et al., 2013b). However, the main pathway for *Synechococcus* to reach fecal pellets was by protozoan grazing upon *Synechococcus*, with subsequent mesozooplankton predation on protozoans. Thus, the indirect pathway through mesozooplankton predation on protozoan grazers of *Synechococcus* was the major pathway for carbon

generated by *Synechococcus* primary production to be exported to depth in zooplankton fecal pellets.

There are also biochemical indications for export of picoplankton-sized particles to the mesopelagic zone by incorporation into sinking particles. Close et al. (2013) found that in surface layers of the North Pacific Subtropical Gyre, lipid profiles, radiocarbon and stable carbon isotope signatures of lipids in submicrometer-sized particulate organic matter (POM) were distinct from those in larger sizes of POM. The distinct lipid signatures of the submicrometer-sized POM dominated total lipids in the mesopelagic zone at 670 m depth. Close et al. (2013) concluded that the lipid components of POM in the mesopelagic had been exported from the epipelagic, presumably by sinking particles in the biological pump.

Marine snow

Origins, abundance, and distributions of marine snow

Macroscopic organic aggregates >500 µm in size, known as “marine snow,” are major components of the biological pump. Marine snow originates from clumps of aggregated phytoplankton (phytodetritus), discarded appendicularian houses, fecal matter, and other miscellaneous detrital particles (Alldredge and Silver, 1988; Kiørboe, 2001; Simon et al., 2002). Aggregation of phytoplankton to form marine snow may also be dependent on bacteria and other microbes in the surrounding water (Grossart et al., 2006). Thus, while aggregated phytoplankton and phytodetritus are important components of marine snow, marine snow also includes other animal, microbial and fecal components that are not phytodetritus.

Marine snow can be ubiquitous and abundant. For a variety of marine and freshwater environments, abundances generally range from <1 to 100 aggregates l⁻¹ (see Table 1 of Simon et al., 2002). On the continental shelf off North Carolina (USA) average marine snow abundance was 125 particles l⁻¹, sinking velocities were 10–150 m d⁻¹, and marine snow comprised >90% of the vertical flux of particulate matter to depth (Shanks, 2002). Alldredge (2005) estimated that the contribution to the total flux of POC from discarded appendicularian houses from *Oikopleura dioica* and *Oikopleura longicauda* alone gave maxima of 12–83% with most values of 28–39%, in several oceanic and coastal regions. In the upper 55 m of the North Pacific Subtropical Gyre, particles from a variety of sources were surprisingly abundant, with peak values of 6–13 particles l⁻¹, but lower values of 0.5–1.0 particles l⁻¹ in oligotrophic areas (Pilskaln et al., 2005).

Marine snow can be associated with physical features such as thin layers or fronts. Large accumulations of marine snow dominated by diatoms have been found in discrete thin layers at density discontinuities in a fjord in the San Juan Islands (Washington, USA) (Alldredge et al., 2002). Möller et al. (2012) photographed dense accumulations of marine snow in thin layers in the Baltic Sea, and copepods were abundantly associated with, and apparently feeding upon these particles of marine snow. Stemmann et al. (2008) found persistent high accumulations of marine snow associated with the Ligurian Sea frontal system in the northwestern Mediterranean. Marine snow can become accumulated in thin layers associated with sharp density gradients by reducing settling speed at density interfaces (Prairie et al., 2013).

Particles and organisms associated with marine snow

Marine snow is colonized by various other living or detrital particles scavenged from the water column. Organisms and particles

associated with marine snow include bacteria, other microbes, various phytoplankters, protozoans, living zooplankton, zooplankton carcasses, abandoned larvacean houses, fecal pellets, macrophyte detritus, and inorganic mineral particles (Simon et al., 2002). Concentrations of such particles in aggregates are highly-enriched relative to the surrounding water column (see Table 2 of Simon et al., 2002). Microbial assemblages on aggregates have higher levels of metabolism, metabolic diversity, and carbon utilization compared to those of surrounding water (Lyons and Dobbs, 2012). In most cases, aggregates are also enriched with nutrients compared to surrounding water (see Table 5 of Simon et al., 2002), which increases the nutritional content of aggregates for their consumers.

Consumption and fragmentation of marine snow by animals

Various animals consume marine snow or particles attached to it. Zooplankton consumers of marine snow include euphausiids (Schnetzer and Steinberg, 2002; Dilling and Brzezinski, 2004) and copepods (Kiørboe, 2001, 2011; Schnetzer and Steinberg, 2002; Koski et al., 2005, 2007; Lombard et al., 2013a; Sano et al., 2013). Both simulations (Kiørboe and Thygesen, 2001; Jackson and Kiørboe, 2004) and experimental observations (Lombard et al., 2013a) suggest that there is a chemosensory component to zooplankton locating and consuming marine snow.

Marine snow can also be fragmented by the activities of zooplankters such as euphausiids (Goldthwait et al., 2004). Such fragmentation can reduce the size of marine snow particles, leading to rapid particle decomposition and leakage of solutes and particulates into surrounding water (Goldthwait et al., 2005; Lombard and Kiørboe, 2010) and reduction of the role of marine snow in the vertical flux to depth (Martin et al., 1987; Karl et al., 1988).

Various fish and fish larvae have been shown to consume macroaggregates. Included are marine (Larson and Shanks, 1996) and freshwater (Kamjunke and Mehner, 2001; Kamjunke et al., 2002) fish. Feeding by fish on macroaggregates links the microbial food web with higher trophic levels because bacteria associated with aggregates can be ingested by fish that cannot ingest suspended bacterioplankton cells (Simon et al., 2002).

Marine snow is also ingested by benthic suspension-feeding bivalves. Newell et al. (2005) found that the blue mussel *Mytilus edulis* ingested marine snow in several embayments along the coast of Maine (USA). Various suspension-feeding bivalves (clams, mussels, oysters, scallops, and others) ingested artificial picoplankton-sized beads that were embedded in marine aggregates (Kach and Ward, 2008; Ward and Kach, 2009). Thus, ingestion of marine snow by benthic bivalves may be a mechanism by which these macroinvertebrates feed upon picoplankton, which are otherwise inefficiently filtered.

Pathogens associated with marine snow

Marine snow can also be a source of pathogens that affect various marine consumers. Marine snow can contain a variety of microbial pathogens. Lyons et al. (2005, 2006) found that marine snow from coastal waters of Cape Cod, Massachusetts (USA) can contain thraustochytrid protist parasites, which infect clams (*Mercenaria mercenaria*) that ingest contaminated aggregates. Lyons et al. (2007) found that marine snow aggregates from various coastal waters of the northeastern United States contained a variety of pathogenic bacteria species, including *Vibrio cholerae* and *Escherichia coli*. Lyons et al. (2010) reported that marine snow and other organic aggregates act as biogeographic islands for microbial aquatic pathogens. Thus, ingestion of such contaminated aggregates by suspension feeders could be a mode of infection for consumers. Marine snow can also be colonized by viruses that

infect and lyse bacteria attached to surfaces (Riemann and Grossart, 2008).

Shapiro et al. (2012) found that the protozoan parasite *Toxoplasma gondii* entered coastal waters off California via terrestrial runoff and could become incorporated into marine snow. Ingestion of contaminated marine snow by marine consumers could provide a means for vectorial intoxication of California sea otters (*Enhydra lutris nereis*) and humans with *T. gondii*.

Phytodetritus

Pulsed export of phytodetritus

Aggregation and pulses of direct sedimentation of phytoplankton from the euphotic zone to depth is an important component of the biological pump. Beginning in the early 1980s the historical notion of a slow steady rain of particulate organic detritus to depth was expanded to include episodic pulses of fast-sinking phytodetritus from sinking phytoplankton blooms, which arrived relatively intact in the deep sea (Deuser and Ross, 1980; Deuser et al., 1981; Billett et al., 1983; Conte et al., 1998, 2001). In a comprehensive review of phytodetritus, Beaulieu (2002) noted dozens of sites in both shallow and deep waters in all ocean basins where phytodetritus pulses had been recorded. In many instances, these pulses represented the majority of the annual input of organic matter from the epipelagic to the benthos. If the amount of phytodetritus reaching the benthos exceeds that which can be processed by the benthic community, then a layer of phytodetrital “fluff” can accumulate on the sea bottom. At many sites, deposition of phytodetritus is a seasonal phenomenon, linked to processes in surface layers such as the spring phytoplankton bloom in temperate waters, the austral summer bloom in the Southern Ocean, or blooms due to seasonal upwelling. Other episodic events of phytodetrital sinking have been linked to surface phenomena such as red tide blooms of dinoflagellates and other harmful algae, or physical processes such as deepening of the upper mixed layer, passage of mesoscale eddies, oceanographic fronts, and ice edge effects (Beaulieu, 2002).

Common phytoplankton components of phytodetrital fluff include diatoms, coccolithophorids, *Phaeocystis* spp., dinoflagellates, and other phytoplankton, fecal pellets, microzooplankton cells and other animal remains, often embedded in larger gelatinous clumps (Beaulieu, 2002). In some cases, intact or viable phytoplankton cells or phytoplankton pigments indicate rapid sedimentation.

Various phytoplanktoners can be dominant components of seasonal deposition of phytodetritus to depth. Diatoms can sink directly to the benthos, particularly a few weeks after spring blooms in surface layers (Billett et al., 1983). Schnetzer et al. (2007) found abundant cells of diatoms of the genus *Pseudo-nitzschia* and the toxin domoic acid from this diatom in particulates in sediment traps at 550 m and 800 m depth after a major toxic *Pseudo-nitzschia* bloom in the San Pedro Channel, California. Coccolithophorids can also form massive surface blooms in temperate and polar waters, which sink to depth (Beaulieu, 2002). Dinoflagellates occasionally contribute to phytodetritus deposition, such as after the 1976 red tide bloom of *Ceratium tripos* in the New York Bight (Mahoney and Steimle, 1979).

Aggregation and disaggregation of phytodetritus and other particles

Sedimentation of phytodetritus is enhanced by aggregation of phytoplankton and other particles, and such phytodetritus can be an important component of the biological pump. There are two types of phytodetritus aggregation, biological and physical. Biological aggregation occurs when animals ingest particles and

incorporate them into fecal pellets. Physical aggregation occurs when smaller discrete particles coagulate by colliding and sticking together to form larger heterogeneous particles (reviews by Alldredge and Jackson, 1995; Burd and Jackson, 2009; Simon et al., 2002). Physical coagulation depends on the concentration, density, size distribution and shape of particles; fluid shear and differential settling velocities that cause particles to collide; and stickiness that holds particles together after collision (Simon et al., 2002). Transparent exopolymer particles (TEP) are important in enhancing the stickiness of phytoplankton cells and other particles that form aggregates (Alldredge et al., 1993; Engel, 2000; Passow, 2002a, 2002b; – see Section ‘Transparent exopolymer particles (TEP)'). Autolysed cytoplasm from cell lysis after cell death can also act as a binding agent in the formation of some diatom aggregates (Armbrecht et al., 2014).

Aggregation is viewed as a major component of the termination and sedimentation of diatom blooms (Burd and Jackson, 2009; Kørboe et al., 1994; Thornton, 2002). Sinking velocities of individual diatom cells are typically $<1\text{--}10 \text{ m d}^{-1}$ (Smayda, 1970), but arrival of diatom phytodetritus on the floor of the deep sea only 2–3 weeks after a surface bloom (Billett et al., 1983) implies sedimentation rates of $100\text{--}150 \text{ m d}^{-1}$. The extent of aggregation of diatoms varies with species, including morphological features such as presence or absence of chain formation or spines, chemical or other environmental conditions, presence or concentrations of microorganisms, and stickiness due to production of extracellular polysaccharides such as TEP (Grossart et al., 2006; Kørboe et al., 1990; Passow, 2002a, 2002b; Yamada et al., 2013).

Aggregation of phytoplankton blooms occurs primarily near the surface, whereas disaggregation through fragmentation, microbial degradation and repackaging by zooplankton feeding occur in deeper waters (Burd and Jackson, 2009). Aggregation and sedimentation of phytoplankton rapidly removes photosynthetically-produced organic matter from surface layers before it can be grazed, and increases food availability to mesopelagic and deep-sea benthic consumers (Alldredge and Jackson, 1995). Aggregation also makes organic matter in small phytoplankton cells more available for consumption by large-particle consumers.

Aggregates have heterogeneous composition. In addition to phytodetritus, aggregates can incorporate fecal pellets, mineral ballast and other particles (Burd and Jackson, 2009). Aggregates have fractal dimensions, and can also be somewhat porous, containing TEP, interstitial water and microorganisms. Thus, the scaling of density with particle size, and therefore the sinking velocity, differs between solid and fractal particles (Burd and Jackson, 2009).

Coagulation can involve both physical and biological aggregation processes. Jackson (2001) combined food web and coagulation models to examine links between physical and biological aggregation. These two processes were found to be non-exclusive or competitive, since fecal pellets could become incorporated into aggregates by physical aggregation (Jackson, 2001).

Disaggregation is the converse of aggregation, and redistributes the contents of larger-sized particles into smaller-sized particles (Burd and Jackson, 2009). Disaggregation is caused by physical processes such as fluid shear, as well as biological processes such as microbial degradation and zooplankton feeding. Physical and biological disaggregation can interact when flow associated with zooplankton swimming breaks up larger aggregates into smaller ones (Dilling and Alldredge, 2000; Goldthwait et al., 2004). Disaggregation can be more important than aggregation, particularly in deeper waters (Dadou et al., 2001; Lepore and Moran, 2007).

Transparent exopolymer particles (TEP)

A previously-unknown class of organic aggregates in the sea known as “transparent exopolymer particles” (TEP) are an

important aspect of phytodetritus aggregation. TEP were first described by Alldredge et al. (1993). These discrete particles are small (3–100s of μm in longest dimension), abundant (10^2 – 10^7l^{-1}), transparent and invisible in light microscopy unless stained by a dye that is specific for acidic polysaccharides (alcan blue), and are formed by exopolymers that are exuded from phytoplankton and bacteria. TEP are sticky, and act as glue in the formation of aggregations of phytoplankton and phytodetritus, as well as marine snow (reviews by Passow, 2002a; Simon et al., 2002). TEP abundances in the water column are similar to those of phytoplankton, and TEP abundances are highest during phytoplankton blooms, particularly those of diatoms.

TEP are formed both biotically and abiotically. TEP can form from sloughing of polysaccharide mucus from cell surfaces of bacteria and phytoplankton (Passow, 2002a). TEP can also form abiotically from dissolved precursors that are released by actively-growing or senescent phytoplankton. Passow (2002b) showed that both bacteria and phytoplankton can contribute to TEP precursors, but phytoplankton is most important for formation of TEP. Diatoms are particularly instrumental in the formation of TEP, and TEP are a major component of diatom aggregates (Passow, 2002a). Gärdes et al. (2011) found that bacteria and diatoms interact in the formation of TEP, in that diatoms had to be photosynthetically-active, and specific diatom-attaching bacteria were required for TEP formation and diatom aggregation.

TEP can also be formed from senescent disintegrating *Phaeocystis* spp. colonies, and can induce deposition events (Reigstad and Wassmann, 2007). Mari et al. (2005) found that during a *Phaeocystis globosa* bloom in experimental mesocosms, while N-limitation induced slow degradation of colonies to non-sticky mucus particles that were exposed to microbial recycling, P-limitation induced rapid disruption of colonies into heavy and sticky mucus aggregates that presumably sank rapidly. Thus, the vertical export versus epipelagic retention fate of a *Phaeocystis* spp. bloom and its associated mucus could depend on the nutrient regime. Nutrient limitation and turbulence can also interact to affect TEP characteristics during blooms (Beauvais et al., 2006; Prieto et al., 2006).

TEP not only sink, but can also ascend in the water column. Azetsu-Scott and Passow (2004) found that laboratory-produced TEP that were free of other particles ascended and accumulated in the surface layers of experimental water columns. However, TEP that had associated mineral particles sank. Thus, the relative proportions of TEP, mineral particles, and interstitial water determined densities of TEP:mineral aggregates, and their sinking or ascending rates. The exchangeable pore-water content of TEP in diatom aggregates can comprise 87–98% of aggregate volume (Ploug and Passow, 2007).

TEP are heavily colonized by bacteria and other microbes, and concentrations of microbes attached to TEP are usually orders-of-magnitude higher than in the surrounding water. Thus, by turning dissolved organic matter into particulate organic matter, which then further aggregates small particles in the water into larger fast-sinking particles, TEP can potentially have major impact on vertical export flux and biogeochemical cycling. Abundance of TEP is related to bacterial abundance and diversity in the mesopelagic Mediterranean (Weinbauer et al., 2013). Ratios of C:N in TEP usually exceed the Redfield ratios (Engel and Passow, 2001). Thus, TEP may provide a mechanism for substantial export and sequestration of carbon at depth (Engel et al., 2002). TEP are also colonized by viruses (Brussaard et al., 2005), which can infect bacteria that have colonized TEP (Mari et al., 2007).

TEP are consumed by various zooplankters. Included are protozoans, appendicularians, euphausiids (references in Passow, 2002a), as well as copepods (Ling and Alldredge, 2003). Because TEP consumed by copepods contained abundant cells of bacteria

and other microorganisms that were too small for copepods to capture individually, TEP appeared to be important as a mechanism by which organic matter can be shunted from the microbial loop to the classical food web and to higher trophic levels (Ling and Alldredge, 2003).

Passow (2002a) noted that the discovery of abundant colloidal and submicrometer-sized TEP in seawater has changed our understanding of the dynamics of the vast pool of DOC in the sea. DOC enters the classical food web through phytoplankton uptake, and is converted to particulate form and transferred to higher trophic levels through a succession of feeding interactions through zooplankton and higher consumers. Within the microbial loop, DOC is taken up by bacterioplankton, and processed by a succession of protozooplankton, mesozooplankton, and higher consumers. Within the “aggregation web” proposed by Passow (2002a), formation of TEP from DOC precursors aggregates small organisms of the microbial loop into larger-sized particles that are large enough to be ingested by mesozooplankton and other larger consumers of the classical food web. This also allows rapid sedimentation of particles attached to TEP that are normally too small to sink, such that they become part of larger fast-sinking particles that sediment to depth in the biological pump.

Concern over warming and increasing concentrations of CO₂ in the atmosphere, and associated ocean acidification has raised questions as to whether the biological carbon pump in the sea will change in efficiency (Passow and Carlson, 2012). Since much of the biological pump is driven by rapidly-sinking aggregates, and TEP are important components of most aggregates, effects of ocean acidification on TEP are potentially important (Mari, 2008; Passow, 2012). Mari (2008) found that addition of acid to seawater within predicted limits of acidification due to increased anthropogenic CO₂ drastically reduced TEP stickiness, and aggregation and sedimentation processes associated with TEP. However, Passow (2012) found that ocean acidification over a range of pre-industrial to predicted future levels had no impact on equilibrium conditions between TEP and their precursors. If the carbonate system was changed by addition of acid, which did not correctly mimic future changes in the carbonate system, TEP levels increased with decreasing pH, likely due to changes in total alkalinity (TA). This implies that abiotic formation of TEP is sensitive to changes in TA, but not pH. Thus, acidification experiments such as those of Mari (2008) may not simulate future changes in ocean acidification. Passow et al. (2014) found that aggregation of POC was independent of three levels of experimental ocean acidification.

Phytodetritus from Phaeocystis spp.

Prymnesiophytes of the genus *Phaeocystis* can form massive blooms of cells in gelatinous colonies, which have been found to sink to depth in various locations. Most *Phaeocystis* deposition events have been recorded for shallow waters, and deposition of *Phaeocystis* phytodetritus to the deep sea is less frequent than for diatoms, likely due to recycling of sinking *Phaeocystis* colonies in the water column (Beaulieu, 2002).

The contribution of *Phaeocystis* spp. phytodetritus to vertical carbon export is usually small (Reigstad and Wassmann, 2007). Compilation of data from polar to sub-arctic and boreal regions revealed that *Phaeocystis* spp. can average 7 ± 11% of export of POC at 30–50 m depth, but a substantial decline occurred from 40–100 m depth, with *Phaeocystis* spp. cell carbon contributing only 3 ± 2% of the POC export to 100 m depth. Even when the carbon contribution of *Phaeocystis* spp. colony mucus was added to carbon of cells, vertical export of POC below 100 m was <5% of the total except for a few cases in which there was unusual deep vertical mixing of *Phaeocystis* spp. colonies to depth (Lalande et al., 2011).

Although grazing of *Phaeocystis* spp. and production of resulting fecal pellets by copepods and other mesozooplankton most likely does not contribute substantially to *Phaeocystis*-originated vertical export flux (Reigstad and Wassmann, 2007), Hamm et al. (2001) found that euphausiid grazing on *Phaeocystis pouchetii* during a bloom in Balsfjord, Norway contributed episodically to increasing the POC flux to depth through rapidly-sinking euphausiid fecal pellets.

Picoplankton in phytodetritus

The assumption that most carbon export to depth comes from large phytoplankton such as diatoms or *Phaeocystis* colonies has been recently re-examined. Models by Richardson and Jackson (2007) suggested that most carbon export in the open sea originates with the picoplankton, which are the most abundant component of the primary production. The relative contribution of picoplankton to export was proportional to the picoplankton contribution to primary production. Using data from the equatorial Pacific Ocean (Richardson et al., 2004) and the Arabian Sea (Richardson et al., 2006), Richardson and Jackson (2007) concluded that picoplankton contributed 70% of the net primary production, 87% of the POC export as detritus, and 76% of carbon exported through mesozooplankton grazing and vertical migration in the equatorial Pacific, and 86% of the net primary production, 97% of the POC export as detritus, and 75% of carbon exported through mesozooplankton grazing and vertical migration in the Arabian Sea.

Stukel and Landry (2010) re-examined the conclusions of Richardson and Jackson (2007) using modeling and data from cruises in the equatorial Pacific. Stukel and Landry (2010) concluded that the contribution of picoplankton to export was proportional to the contribution to primary production, but that the mean contribution of picoplankton to export was comparatively low (23%), compared to the contribution estimated by Richardson and Jackson (73%). These differences were somewhat due to sensitivities within the models.

The summer export pulse (SEP) of phytodetritus in the subtropical north pacific

There is recent evidence from the North Pacific for predictable seasonal episodic export of phytodetritus to depth, apparently due to photoperiodism (day length) associated with the summer solstice. A 13-year (1992–2004) sediment trap time-series from the HOT Program at Station ALOHA off Hawaii (Karl et al., 2012) revealed that every summer (July 15–August 15) there is a large, rapid, and predictable pulse in particulate organic matter export to 4000 m depth. This summer export pulse (SEP) is 3× larger than mean wintertime particle fluxes, and fuels more efficient carbon sequestration because of low remineralization during rapid downward transit, leading to elevated carbon:phosphorus ratios. Peak summertime molar ratios of POC:P and PN:P are 257:1 and 22:1, respectively – well above the Redfield ratios of 106:1 and 16:1. The ratios are due to the SEP being enriched in carbon and nitrogen, relative to phosphorus. This enrichment is due to seasonal changes in the microbial assemblage, namely summertime increases in symbiotic nitrogen-fixing cyanobacteria in association with diatoms (*Richelia* sp.). Chlorophyll/phaeopigment ratios are consistent with fresh organic matter being delivered to 4000 m depth.

This SEP is predictable in time despite oceanographic features such as storm-induced mixing, mesoscale eddies, and atmospheric deposition of nutrients that vary between years. Karl et al. (2012) hypothesized that changes in day length (photoperiodism) may be an important environmental cue to initiate aggregation and subsequent export of organic matter to the deep sea. At Station ALOHA (22°45'N, north of Hawaii), the sun is directly overhead

twice a year: in early June as it moves north toward the Tropic of Cancer, and again on July 5 as the sun moves back south toward the Tropic of Capricorn. For a 3-week period from June 11 to July 1, the sun is essentially overhead of this station, and there is an almost constant daylength of 13.52–13.53 h. After July 1, there is an abrupt loss of daylength of 10–15 min/week.

This highly-predictable change in daylength may be the trigger for changes in diatom populations (aggregation, gamete formation) that result in the SEP. Because nearly all marine cyanobacteria and eukaryotic phytoplankton, including diatoms, have phytochromes (cytoplasmic pigments in autotrophs that absorb light and mediate processes such as dormancy, greening of leaves, sexual reproduction), marine phytoplankton may be subject to light-activated molecular switches caused by astronomical events. These results highlight how little is known of some fundamentally-important ecological features of the planet.

Benthic community responses to phytodetritus

Deep-sea benthic communities respond in various ways to episodic and/or seasonal pulses of surface-derived phytodetritus. Benthic community responses to pulses of phytodetritus include timing of reproductive periodicities of benthic animals, increases in sediment community oxygen consumption, increased microbial activity, and benthic animal recycling patterns that were coincident with enhanced sedimentation of organic matter. Early studies of such benthic community responses to phytodetritus were reviewed by Beaulieu (2002), Turner (2002), and Rowe (2013). Recent studies summarized below have noted additional examples of benthic responses to phytodetritus pulses.

At an abyssal site (4850 m depth) in the Porcupine Abyssal Plain in the northeast Atlantic, there were responses by benthic animals to episodic phytodetritus pulses. Vanreusel et al. (2001) found evidence for episodic recruitment of infaunal polychaetes, and Witbaard et al. (2001) found enhanced grazing by the holothuroid *Oneirophanta mutabilis* in response to seasonal deposition of phytodetritus to the sediments. Bett et al. (2001) noted “a radical change in abundance and activity of megabenthos” between two three-year periods (1991–1994 and 1997–2000) of summer sampling that was characterized by differences in mass depositions of aggregated phytodetritus. During 1991–1994, there was mass deposition of phytodetritus, and the megabenthos completely exploited the food on the surface of the seabed over a period of 2.5 years. However, during 1997–2000, there was no mass deposition of phytodetritus observed with time-lapse photography, but the megabenthos increased dramatically in abundance, and completely exploited the food on the surface of the seabed in just 6 weeks. Bett et al. (2001) suggested that the increases in megabenthos abundance and activity rapidly removed incoming phytodetrital flux from the seabed during 1997–2000. Lampitt et al. (2001) concluded that the differences in phytodetritus accumulation on the sea bed between these two periods were likely due to rapid consumption of phytodetritus by megabenthos rather than to differences in rate of supply from above.

Smith Jr. et al. (2002) found several indications of benthic responses to seasonal phytodetritus pulses at 4000 m at the HOT station in the North Pacific subtropical gyre. These included peak fluxes of POC and particulate nitrogen, and increased sediment organic carbon, total nitrogen, and phaeopigments in September 1998, corresponding to pulses in fluxes of particulate matter. Abundance of bacteria, foraminiferal fragments and metazoa in surface sediments were also all maximal during this period (Smith Jr. et al., 2002).

Long time-series studies off the coast of California also reveal connections between surface phytoplankton productivity as measured by climate indices, and phytodetritus pulses to depths of

over 4000 m. Ruhl and Smith Jr. (2004) and Smith Jr. et al. (2006a, 2006b, 2008a, 2008b, 2008c) found that there were direct relationships between upwelling intensity near the surface and phytodetritus export to depth. Vardaro et al. (2009) found periodic variations in abyssal sediment bioturbation by the echinoid *Echinocrepis rostrata* that were correlated with episodic pulses of particulate organic carbon. Kahn et al. (2012) also noted increases in abundance of deep-sea sponges at this site that were correlated with episodic pulses of particulate organic carbon.

Smith Jr. et al. (2013) found that after 24 years of the time-series study of deep-sea benthic responses to export flux in the northeast Pacific, previous findings of food deficits in the supply of surface-originating food reaching the benthos were questionable. During the last two years of the data (2011–2012), large episodic pulses of sedimentation provided surpluses of POC that met benthic utilization. These pulses to the benthos were associated with epipelagic increases in primary productivity, which were associated with upwelling that was possibly enhanced by increased wind stress, due to climate change. During 2011–2012, the densities of mobile animals on the seafloor (primarily holothurians) at this station increased by nearly an order of magnitude, with some species exhibiting the highest densities recorded during the 24-year time-series (Kuhnz et al., 2014).

A large salp bloom in the northeast Pacific during spring of 2012 caused a major deposition of salp detritus and fecal pellets to the sea bottom at 4000 m depth (Smith Jr. et al., 2013a, 2013b, 2014a, 2014b). POC flux to the bottom increased sharply in early spring of 2012, and salp detritus covered much of the seafloor (maximum = 98%) during the following summer. There were also increases in sediment community oxygen consumption (SCOC) and in the abundance of a benthic holothurian during the period after salp deposition. Food supply provided by salp detritus was estimated to provide 97–327% of the SCOC demand over the 6-month period after the salp bloom. Smith Jr. et al. (2014a, 2014b) concluded that large episodic pulses of food deposition such as during the 2012 salp bloom can provide food for abyssal benthic communities for months if not years.

Several recent studies have confirmed that microbial and benthic animal consumption of phytodetritus can be rapid. Moodley et al. (2005) found that bacteria were important in the rapid respiration of fresh phytodetritus at several deep-sea sites in the Mediterranean and northeast Atlantic. Sweetman and Witte (2008) similarly found that deep-sea macrofauna (cumaceans and polychaetes) rapidly consumed labeled phytodetritus off California. Jeffreys et al. (2011) found that deep-sea fish in the northeast Atlantic, but not in the Mediterranean ingested phytodetritus. However, Veit-Köhler et al. (2011) found that neither meiofauna nor bacteria in the deep (2960 m) Southern Ocean increased in abundance in response to phytodetritus from a sinking phytoplankton bloom, and suggested that the delayed response was due to cold temperatures.

Other components of the biological pump

Fish fecal pellets and fish-mediated export

Fecal pellets from fish and fish-mediated export of POC may be much more important in the biological pump than previously realized. Sinking velocities of fish fecal pellets can reach $>10^3 \text{ m d}^{-1}$ (Bray et al., 1981; Robison and Bailey, 1981; Saba and Steinberg, 2012; Staresinic et al., 1983), particularly in upwelling areas where small planktivorous fish are abundant. However, there have been few previous studies of the importance of fish fecal pellets.

Saba and Steinberg (2012) determined abundance, sinking rates, particulate organic carbon and nitrogen contents, and prey

composition in fecal pellets produced by forage fish (likely the northern anchovy *Engraulis mordax*) in the seasonal upwelling region of the Santa Barbara Channel, California. Fish fecal pellets were abundant (up to 5.9 m^{-3}), large (1 mm in diameter and 1–6 mm long), and filled with remains of plankton prey, including dinoflagellates, diatoms, silicoflagellates, ciliates, and copepods. Pellets had amounts of POC and particulate nitrogen relative to volume that were similar to copepods and salps. Fecal pellets had rapid sinking velocities ($458\text{--}1370 \text{ m d}^{-1}$). These speeds were faster than recorded sinking velocities for fecal pellets of euphausiids, but similar to those of salps and mesopelagic fish. Saba and Steinberg (2012) estimated that the downward flux of POC due to fish fecal pellets exceeded previous measurements of total sediment trap POC flux. Estimated fish fecal pellet flux could exceed total trap POC flux if the traps missed episodic pulses of fish fecal pellets. Saba and Steinberg (2012) concluded that fish fecal pellets transported substantial amounts of repackaged surface material to depth in their study area.

Fish-mediated active transport may also be an important component of the biological pump. Davison et al. (2013) estimated “fish-mediated export” (FME) of carbon from the euphotic zone through the vertical migration activities of mesopelagic fish in the California current and North Pacific. FME included estimates of respiration, fecal production and fish mortality, with estimates based on individual-based metabolic modeling and catch data from mesopelagic trawls. FME ranged from 15% to 17% of total carbon exported to depth, but varied in magnitude and relative importance over the study area. Due to the vertical migratory behavior of these mesopelagic fishes, their daytime residence depths were below the depths where most remineralization of particles falling from the epipelagic occurs. Thus, FME was approximately equal to passive sinking of particles at a depth of 400 m. Davison et al. (2013) estimated that the active transport of carbon by mesopelagic fishes and zooplankton was similar to the discrepancy between estimates of carbon export from sediment traps or thorium disequilibrium techniques, and by other methods such as nutrient and oxygen budgets. Davison et al. (2013) concluded that FME should be considered in models of the global carbon cycle.

The importance of fish in the biological pump depends on the abundance of fish in the sea. A recent report by Irigoien et al. (2014) suggests that global fish biomass has been severely underestimated. Using acoustic methods on a circumglobal research cruise, the biomass of fish in the mesopelagic zone (200–1000 m) was estimated to be at least an order-of-magnitude higher than previous estimates. Irigoien et al. (2014) estimated that the role of mesopelagic fish in the biological pump needed revision, because in deep waters, these fish may be respiring 10% of surface-layer primary production.

Sinking carcasses of animals and macrophytes

Sinking carcasses of animals and macrophytes, including episodic mass deposition events of small animals such as zooplankton, as well as sporadic, rare sinking of carcasses of large nekton or macroalgae can contribute to the biological pump. Mass deposition of zooplankton carcasses have been observed for several taxa. Included are copepods (Frangoulis et al., 2011; Sampei et al., 2012), pyrosomes (Lebrato and Jones, 2009), larvaceans (Robison et al., 2005), salps (Henschke et al., 2013; Smith Jr. et al., 2014a, 2014b), pteropods (Tsurumi et al., 2005), and jellyfish (Billett et al., 2006; Lalande and Fortier, 2011; Lebrato et al., 2011; Riemann et al., 2006; Sweetman and Chapman, 2011; Titelman et al., 2006; Yamamoto et al., 2008). Sampei et al. (2009a) found that passively-sinking copepod carcasses contributed 36% of the overall annual export flux of particulate organic carbon in the Beaufort Sea.

[Lebrato et al. \(2013\)](#) concluded that sinking of gelatinous zooplankton particulate organic matter was an important component of the biological pump. Sinking rates and decomposition rates were measured for gelatinous particulate organic matter (jelly-POM) from several different species of scyphozoans, ctenophores, thaliaceans, and pteropods, in order to estimate export efficiencies of jelly-POM. Export efficiencies were estimated for jelly-POM sinking from 200 m and 600 m in temperate, tropical and polar environments. Jelly-POM sank at means of 850–1500 m d⁻¹, with polar waters representing fast-sinking, low-decomposition situations, regardless of species. Tropical and temperate waters had substantial decomposition above 1500 m, unless jelly-POM sank below the permanent thermocline. [Lebrato et al. \(2013\)](#) concluded that jelly-POM represents a substantial and underappreciated component of the biological carbon pump worldwide.

[Takahashi et al. \(2013\)](#) described a unique predation interaction between sapphirinid copepods and gelatinous doliolids that may enhance sinking particulate carbon flux. The copepod *Sapphirina nigromaculata* was observed to actively prey on *Dolioletta gegenbauri* in the Kuroshio Extension. Copepods chewed through and entered doliolid body cavities, leaving characteristic bite marks, and copepods then ingested internal tissues of doliolids. Doliolid carcasses with the same characteristic bite marks were recovered in sediment traps at 50 m depth. Discarded doliolids were estimated to comprise 0.8% of the POC flux recorded for sediment traps.

Decomposition of sunken carcasses or macrophytes contributes to deep-sea food webs. Dead jellyfish stimulated the microbial communities in a Norwegian fjord ([Riemann et al., 2006](#); [Titelman et al., 2006](#)). Amphipods scavenged dead fish in baited camera studies in the Arctic ([Premke et al., 2006](#)), and fish efficiently scavenged dead porpoise carcasses in the northeast Atlantic ([Kemp et al., 2006](#)). Whale carcasses are scavenged by various benthic fauna, including nematodes and polychaetes ([Braby et al., 2007](#); [Dahlgren et al., 2004, 2004](#); [Goffredi et al., 2004](#); [Lundsten et al., 2010a, 2010b](#); [Smith and Baco, 2003](#); [Smith et al., 2014](#)). Deep-sea fish have been photographed consuming spinach ([Jeffreys et al., 2010](#)), and *Sargassum* or mackerel bait at the bottom of the North Atlantic ([Fleury and Drazen, 2013](#)).

[Pershing et al. \(2010\)](#) calculated that removal of large whales by whaling has reduced the ocean's biological pump and storage of carbon. Living populations of large baleen whales now store >9 million tons less carbon than before whaling. If whale populations could be restored to pre-industrial whaling levels, [Pershing et al. \(2010\)](#) estimated that sinking of whale carcasses would export >200,000 tons of carbon to depth each year.

Feces from marine mammals

Feces from marine mammals may be an important component of the biological pump. Sperm whales (*Physeter macrocephalus*) in the Southern Ocean may be contributing to the biological pump by helping to remove atmospheric carbon dioxide rather than contributing to it through respiration ([Lavery et al., 2010](#)). Sperm whales feed at depths below the euphotic zone, but defecate near the surface, because they shut down non-crucial biological functions while diving. Further, unlike zooplankton and fish which produce fast-sinking fecal pellets, the feces of sperm whales is mostly liquid, which disperses into the waters of the euphotic zone. This feces is rich in iron, and phytoplankton photosynthesis in the Southern Ocean is mostly iron-limited. Thus, feces from sperm whales can stimulate phytoplankton production in the euphotic zone. This phytoplankton production is then grazed by zooplankton and the carbon in it is exported to depth in sinking zooplankton fecal pellets. [Lavery et al. \(2010\)](#) calculated that the current populations of 12,000 sperm whales in the Southern Ocean act as

a carbon sink, removing 2×10^5 tons more carbon than they add through respiration. [Lavery et al. \(2010\)](#) concluded that human hunting of sperm whales has likely reduced the export of carbon to depth in the Southern Ocean.

Feces from other marine mammals may also be important in providing nutrients for phytoplankton. [Roman and McCarthy \(2010\)](#) calculated that nitrogen in flocculent fecal plumes from whales and seals may contribute more nitrogen to the euphotic zone of the Gulf of Maine than the input of all of the region's rivers combined. [Smith et al. \(2013\)](#) found that feces from the pygmy blue whale *Balaenoptera musculus brevicaudata* stimulated photosynthetic performance and growth of three phytoplankton species, the ubiquitous chlorophyte *Dunaliella tertiolecta*, the Southern Ocean diatom *Chaetoceros pendulus*, and the Antarctic prymnesiophyte *Phaeocystis antarctica*.

The biological pump and climate

The biological pump has been, is, and will be influenced by, and has had, has, and will have influence on global climate during periods of the Earth's past, present and future, respectively.

Origins of the biological pump

The biological pump appears to have been in operation in the ocean for over a half-billion years. [Tziperman et al. \(2011\)](#) and [Ridgwell \(2011\)](#) have speculated on the origin of the biological pump in the ocean. They suggest that this process has only existed during the Phanerozoic (the most recent 540 million years since the Cambrian "explosion" of life recorded in the fossil record). Prior to this, during the Neoproterozoic (1 billion–540 million years ago), there were extreme glacial episodes when the global ocean potentially had complete sea ice cover known as "snowball Earth." Patterns of carbon cycling and oxidizing organic matter in the sea may have undergone profound changes at this time, resulting in the biological pump of the last half-billion years.

The Precambrian ocean was less well-oxygenated than at present. Thus, some of the DOM that is now rapidly degraded could have become refractory then. Both atmospheric and ocean reservoirs of inorganic carbon would have been larger, but both were potentially dwarfed by the size of the ocean DOM pool.

Once oxygen from the activities of cyanobacterial photosynthesis built up to oxygenate the atmosphere and ocean to levels approaching those of the Phanerozoic, this would have reduced the high levels of atmospheric CO₂, leading to cooling and therefore snowball Earth. Oxygenation of the ocean would allow evolution of protists and metazoans, and development of the biological pump in which there is a strong vertical settling flux of particulate organic matter that decreases exponentially with depth due to aerobic degradation in oxygenated waters. Late Proterozoic diversification of marine eukaryotes (which began 800 million years ago) may have facilitated the episodic biological pump by causing greater proportions of organic matter to be in the form of larger aggregates that sank more efficiently, due to increased size.

The global glaciations may have resulted from enhanced export of organic matter from the upper ocean into anoxic subsurface waters and sediments. This organic matter would have undergone anoxic remineralization at depth by either sulfate- or iron-reducing bacteria. Both could have led to changes in ocean carbonate and dissolved inorganic carbon pools that would have drawn down atmospheric CO₂ into the ocean, which would have caused global cooling and glaciation. However, once the oceans became more oxygenated, this changed the anoxic remineralization chemistry in the deep sea, preventing the biogeochemical mechanism that

initiated the Neoproterozoic “snowball Earth” glaciations from doing so again.

The biological pump may have also cooled the Earth ending a previous “greenhouse climate” (Bains et al., 2000). The onset of the Paleocene/Eocene thermal maximum approximately 55 million years ago saw global surface temperatures rising by 5–7 °C over a period of approximately 30 thousand years, probably due to mantle outgassing of methane and CO₂ (Zachos et al., 2003). The response of the planet appears to have been intensified export flux through the biological pump, which cooled greenhouse climate by rapid removal of excess CO₂ from the atmosphere (Bains et al., 2000).

The biological pump and glacial/interglacial cycles

The biological pump appears to have contributed to variations in levels of atmospheric CO₂ during glacial/interglacial episodes during the ice ages of the Pleistocene period. Concentrations of atmospheric CO₂ recorded in ice cores were lower during glacial periods than during interglacial periods (Sigman and Boyle, 2000). Because climate models of physical processes are unable to reproduce the observed decreases in atmospheric CO₂ levels in glacial periods, changes in the biology of the ocean, including the biological pump, are hypothesized to have been instrumental in glacial atmospheric CO₂ drawdowns.

During most of the Holocene, roughly the last 10000 years, the atmospheric partial pressure of CO₂ (=atmospheric concentration of CO₂) has been near 280 ppm by volume (p.p.m.v.), whereas during the Last Glacial Maximum about 18000 years ago, atmospheric partial pressure of CO₂ was 180–200 p.p.m.v., or 80–100 p.p.m.v. lower. The causes for such variations in atmospheric CO₂ are unresolved, but are thought to be due to the ocean's biological pump (Sigman and Boyle, 2000).

The deep ocean pool of dissolved inorganic carbon is over an order-of-magnitude greater than the combined amounts in the terrestrial biosphere and soil carbon reservoir, the atmospheric CO₂ reservoir, and the warm upper ocean. Also, because deep-ocean water is exposed to the surface only about every 1000 years, changes in concentrations of atmospheric CO₂ driven by anything other than the ocean would be diluted into the deep-ocean pool of DIC, attenuating atmospheric changes over the time scales of glacial/interglacial periods (Sigman and Boyle, 2000). Thus, glacial/interglacial changes in levels of atmospheric CO₂ must be due to processes in the ocean (Broecker, 1982a).

Potential explanations for the variations in atmospheric CO₂ include changes in terrestrial carbon storage, ocean temperature, and changes in ocean alkalinity or the marine calcium carbonate budget. These processes appear to be insufficient to explain the magnitude of the recorded glacial/interglacial variations in atmospheric CO₂ levels (see arguments in Sigman and Boyle, 2000).

Broecker (1982b) first proposed that the main cause of lower levels of atmospheric CO₂ during glacial periods was strengthening of the ocean's biological pump, due to differences in the nutrient chemistry of seawater during glacial periods. One such change would be increases in nitrate and phosphate in low-latitude surface waters where current low levels of these nutrients limit biological production and export flux to depth. However, estimates of the effects of such increases are insufficient to account for the observed declines in atmospheric CO₂ levels during glacial periods (Sigman and Boyle, 2000). Another mechanism would be enhanced biological production and export flux through more complete utilization of high levels of nutrients in high-latitude waters, where much of the current inventory of nutrients remains unused (Sigman and Boyle, 2000).

There may have been large glacial/interglacial changes in nitrogen levels due to denitrification and/or nitrogen fixation (Gruber

and Sarmiento, 1997). Falkowski (1997) has proposed that nitrogen fixation was greater during glacial periods due to increased levels of airborne dust, which added iron to the ocean, and enhanced nitrogen fixation. Thus, decreases in water-column denitrification, and increases in nitrogen fixation may have led to greater export production through the biological pump, potentially explaining glacial/interglacial variations in atmospheric CO₂ levels (Falkowski, 1997; Ganeshram et al., 1995; McElroy, 1983). Increases in suboxic zone denitrification during transitions from glacial to interglacial periods have been associated with rapid increases in atmospheric CO₂ (Altabet et al., 2002; Devol, 2002), and similar global expansion of suboxic water due to denitrification caused by ocean acidification have been predicted for the future (Oschlies et al., 2008).

Processes in the high-latitude oceans, particularly the Southern Ocean, are thought to account for increases in efficiency of the biological pump during glacial periods (Sigman and Boyle, 2000). Surface water sinks to depth in high-latitude waters, ventilating the deep ocean. Upwelling at subpolar latitudes brings deep waters that are high in nutrients and CO₂ to the surface, where they are exposed to the atmosphere, and CO₂ is released to the atmosphere. High nutrients in upwelled waters fuel surface-layer primary production, increasing export flux to depth. This lowers the partial pressure of CO₂ in surface waters, causing the surface waters to reabsorb some of the atmospheric CO₂ that had initially leaked out of the upwelled waters, thereby lowering levels of atmospheric CO₂ in glacial periods (Sigman and Boyle, 2000). Thus, high-latitude surface ocean waters that ventilate the ocean interior, such as the Southern Ocean, may affect atmospheric levels of CO₂ through variations in the biological pump.

Sigman and Boyle (2000) proposed a mechanism whereby lower glacial atmospheric CO₂ concentrations were caused by reduced deep-water ventilation and enhanced nutrient utilization. A northward shift and decrease in strength of the eastward winds would have decreased upwelling of deep water into the surface layers of the Antarctic, reducing deep water ventilation, epipelagic nutrient supply and CO₂ outgassing. Export production may have increased in the subantarctic, possibly due to iron from dust. Sigman and Boyle (2000) concluded that the most likely cause of glacial/interglacial changes in atmospheric levels of CO₂ involved extraction of carbon from the surface ocean by biological production and the biological pump.

Reasons for the drawdown of atmospheric CO₂ during glacial cycles remain elusive. Kohfeld et al. (2005) analyzed sedimentary records of marine phytoplankton productivity during the last glacial cycle, and found that neither changes in nutrient utilization in the Southern Ocean nor shifts in dominant plankton types could explain the drawdown of atmospheric CO₂ by 80–100 p.p.m.v. Iron fertilization through increased atmospheric deposition and associated mechanisms could account for no more than half of the observed drawdown of atmospheric CO₂. Thus, Kohfeld et al. (2005) concluded that a combination of biological and physical mechanisms must have caused the drawdown.

Sigman et al. (2010) noted that in the modern Southern Ocean, high-nutrient CO₂-rich water from depth ascends into the surface layer and returns to depth before nutrients are fully depleted by phytoplankton photosynthesis. This incomplete utilization of nutrients allows CO₂ that was sequestered at depth to leak into the atmosphere. This “Southern Ocean leak” may have been reduced during ice ages due to changes in nutrient and physical regimes that altered the efficiency of the biological pump (Sigman et al., 2010).

The efficiency of the biological pump varies with latitude (Sigman et al., 2010). Highest efficiency is in the vast low-latitude low-nutrient surface waters, where nutrient-replete water that is upwelled or mixed from depth into the euphotic zone becomes

stripped of nutrients by photosynthesis. The resulting POC then sinks or is transported downward by the biological pump to become “regenerated” nutrients, and CO₂ that is sequestered at depth, away from the atmosphere (Sigman et al., 2010). The biological pump has lowest efficiency in high-latitude high-nutrient surface waters, currently found mostly in the Southern Ocean, where nutrient- and CO₂-rich water ascends from depth, and descends again with most of the “preformed” nutrients (Ito and Follows, 2005) remaining. This process causes the “Southern Ocean leak” (Sigman et al., 2010) into the atmosphere of CO₂ that had been dissolved in the deep sea.

The strengths of the biological pump and atmospheric CO₂ leak have varied over time for different regions of the Southern Ocean. During the last ice age the strength of the biological pump was apparently reduced compared to the present in the Antarctic zone south of the Antarctic Circumpolar Current, but in the Subantarctic Zone north of the Antarctic Circumpolar Current the biological pump was stronger than today (Jaccard et al., 2013; Kumar et al., 1995; Mortlock et al., 1991; Sigman et al., 2010). This increased Subantarctic Zone export production during ice ages coincided with increasing dust fluxes from Patagonian deserts, suggesting that iron fertilization of subantarctic phytoplankton may have increased the biological pump and atmospheric CO₂ drawdown (Jaccard et al., 2013; Kumar et al., 1995; Martin, 1990; Martínez-García et al., 2014). Thus, the air-sea balance of CO₂ is controlled mainly by the biological pump and circulation of the deep-water formation region of the Antarctic Zone, whereas global export production is controlled mainly by the biological pump and intermediate water formation region of the Subantarctic Zone (Marinov et al., 2006).

Sigman et al. (2010) concluded that biological pumps in different regions of the Southern Ocean were important factors in glacial/interglacial changes in atmospheric CO₂. A possible control valve in the Southern Ocean leak of atmospheric CO₂ was the circulation-related release of CO₂ sequestered in the deep ocean through the surface waters of the Southern Ocean. Reduced water exchange between the Antarctic surface waters and the underlying deeper layers may have closed this valve during the last ice age. This, coupled with increased subantarctic phytoplankton productivity, possibly due to iron enrichment, may have more efficiently utilized other surface-layer nutrients, with the biological pump transporting CO₂ to depth. The combination of these and other possible mechanisms or factors (ice coverage, differential phytoplankton nutrient consumption, CaCO₃ dissolution and alkalinity change, shoaling of North-Atlantic deep water isolating and reducing ventilation of the deep ocean) would have had the overall effect of separation of the ocean during the last ice age into a “slowly ventilated, CO₂-rich deep ocean most directly under the control of a stratified and/or ice covered Antarctic and”...“a nutrient-poor and CO₂-poor upper ocean ventilated by the North Atlantic and the more equatorward regions of the Southern Ocean” (Sigman et al., 2010). Fluctuating levels of carbon in the deep sea during glacial periods may also be due to alternating cycles of ventilation of the deep sea by waters sinking from the Southern Ocean and the North Atlantic (Skinner et al., 2014) or expansion of Antarctic sea ice which reduces exchange of carbon between the ocean and the atmosphere (Ferrari et al., 2014).

Because sinking diatoms are important components of the biological pump, silica is required for diatom growth, and the Southern Ocean is the circulation hub for the global ocean, the dynamics of silicic acid in the Southern Ocean can have far-reaching effects on diatom dynamics, the biological pump, and atmospheric levels of CO₂ elsewhere (Dugdale and Wilkerson, 2001; Sarmiento et al., 2003). These parameters may have been different during ice ages (Pichevin et al., 2009). Since the biological pump strips nutrients out of epipelagic waters and exports nutrients to

depth, if there were no return of nutrients from deep waters into the euphotic zone, the biological pump would eventually deplete nutrients from the euphotic zone, and phytoplankton primary productivity would collapse. The main return path from deep waters for silicic acid and other nutrients is upwelling in the Southern Ocean, with subsequent nutrient entrainment into sinking Subantarctic Mode Water (SAMW), which sinks from the Subantarctic Zone north of the Antarctic Polar Front Zone and spreads northward into the entire Southern Hemisphere and North Atlantic (Sarmiento et al., 2003). Because silica in diatom shells that sink from northward-moving surface waters is returned from depth to the surface in southward-moving waters that are upwelling at the Antarctic divergence, this vertical recycling loop between surface and deep waters supports heavy diatom growth and forms a global silicon trap in the Southern Ocean (Assmy et al., 2013). The abundant silicic acid in the Southern Ocean may have resulted in the evolution of thick silica frustules in some taxa of Antarctic diatoms, which may serve as body armor to deter copepod grazers (Assmy et al., 2013; Boyd, 2013). Such thick-shelled diatoms may export more silica than carbon through the biological pump, whereas thinner-shelled taxa, when stimulated by iron fertilization, export more carbon than silica (Assmy et al., 2013; Boyd, 2013).

This sequestration of silicon in the Southern Ocean causes silicic acid limitation of diatom growth elsewhere, particularly in the equatorial Pacific, which is a main source of outgassing of atmospheric CO₂ (Dugdale and Wilkerson, 2001; Pichevin et al., 2009). A decline in accumulation rates of opal in glacial sediments of the Eastern Equatorial Pacific (EEP) may have resulted from reduced levels of silicic acid, but increased levels of iron from continental dust input, which stimulated primary productivity and invigorated the biological pump in the EEP, contributing to the recorded declines in atmospheric CO₂ during glacial periods (Pichevin et al., 2009).

The biological pump and contemporary climate variations

The biological pump and the deep sea are strongly impacted by contemporary climate variation. Export flux of POC and changes in deep-sea benthic communities correlate with several indices of contemporary climate variability (reviewed by Smith Jr. et al., 2009). These correlations suggest that climate-related variations in the delivery of detrital food to depth by the biological pump affects variations in benthic community abundance and species composition (Ruhl et al., 2008).

Ruhl and Smith Jr. (2004) recorded a major change in community structure of dominant epibenthic echinoderms at 4100 m depth in the northeast Pacific off California, and this change was synchronous with a major El Niño/La Niña episode between 1997 and 1999. Two dominant taxa of holothuroids decreased in abundance by 2–3 orders of magnitude, whereas six other species of holothuroids, echinoids and ophiuroids increased in abundance by 1–2 orders of magnitude. These shifts in abundance correlated with three different indices related to El Niño/La Niña events: the Northern Oscillation Index (NOI), the Southern Oscillation Index (SOI), and the Multivariate El Niño-Southern Oscillation Index (MEI). Cross-correlation coefficients between climate and abundance of all five species of holothuroids peaked with abundance lagging climate by 11–22 months. The NOI, SOI, and MEI climate indices also had significant time-lagged correlations with POC flux to the sea floor. Together, all of these correlations suggest that the abyssal benthic community was responding to climate-related pulses of detrital food delivered by the biological pump. Using samples from the same time-series study as Ruhl and Smith Jr. (2004), Wilson et al. (2013) found that the proportion of total POC in identifiable fecal pellets exported to depth was negatively

correlated to overall POC flux, and to indicators of climate variability such as the North Pacific Gyre Oscillation (NPGO) and the NOI. Wilson et al. (2013) suggested that the inverse correlations between these climatic indices and proportions of POC due to fecal pellets were due to variations in community structure of the zooplankton producing the pellets, particularly the relative proportions of larvaceans versus copepods.

Ruhl and Smith Jr. (2004) noted that Billett et al. (2001) had recorded a similar shift in abundance in epibenthic megafauna in response to climate variation and POC flux on the Porcupine Abyssal Plain (PAP) in the northeast Atlantic. Using data of Lampitt et al. (2001) on POC fluctuations from the same PAP study that produced the data of Billett et al. (2001), Ruhl and Smith Jr. (2004) found significant correlations (time-lagged by 5 months) between POC flux and the North Atlantic Oscillation (NAO) index. Thus, Ruhl and Smith Jr. (2004) suggested that climate variation represented by indices for El Niño/La Niña in the North Pacific, or the NAO in the northeast Atlantic, may strongly influence variations in delivery of detrital food to depth by the biological pump, and that food variability may be reflected in patterns in deep-sea megafauna.

The NAO also appears to be related to the biological pump in the Sargasso Sea. Lomas et al. (2010) found that from 1996 to 2007 there was a decade-long increase of >50% in euphotic zone total chlorophyll *a*, prokaryotic phytoplankton abundance, primary production and POC export flux through 150 m depth that coincided with a shift of the winter NAO index from consistently positive to neutral but variable. This followed a strong shift in the NAO from positive to negative during winter of 1996. The shift in the NAO to more negative values after 1996 reflected increases in the frequency of westerly wind events, which caused more frequent vertical mixing of the ocean's upper mixed layer. Counterintuitively, the export flux increased with a shift from larger to smaller phytoplankton, during a decline in proportions of diatoms and increase in proportions of picoplanktonic *Synechococcus*. Lomas et al. (2010) suggested that the diatom decline might be due to changes in proportions of various nutrients, increases in dissolved inorganic carbon due to ocean acidification, or preferential grazing on diatoms by vertically-migrating mesozooplankton, which were also increasing during daytime at shallow depths during the period 1996–2007. The increases in POC flux during periods of picoplankton dominance suggest that particle aggregation might have contributed to the increased POC export flux. Lomas et al. (2010) concluded that in the oligotrophic North Atlantic there was strong coupling between increased primary production and export flux from the euphotic zone and its attenuation in the mesopelagic zone, such that both parameters increased following enhanced vertical mixing due to shifts in the NAO.

The NAO also appears related to storage and uptake of anthropogenic CO₂ in the North Atlantic. Simulations by Levine et al. (2011) suggest that the strong influences of the NAO on mixing of surface waters to depth alter the residence time of anthropogenic CO₂ in the North Atlantic through changes in water mass transformations. This downward mixing may transport anthropogenic CO₂ from surface layers to the ocean interior where anthropogenic CO₂ is retained.

Biological responses to climatic forcing have also been noted in the subtropical North Pacific (Bidigare et al., 2009; Corno et al., 2007). At Station ALOHA during the period 1990–2004, observations and modeling revealed that there were substantial increases in primary productivity, upward flux of nitrate into the euphotic zone, and downward flux of particulate nitrogen to depth. There were concurrent increases in epipelagic cyanobacteria, eukaryotic phytoplankton and zooplankton biomass during this period. These biological responses were due to climatic forcing that coincided with changes in the El Niño/Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) indices, which destratified the upper

layers of the ocean, with associated increased wind mixing and nutrient injection into the euphotic zone. Bidigare et al. (2009) concluded that climatic forcing of variations in nitrate flux, plankton abundance and composition can regulate particulate export over interannual and decadal periods.

The biological pump and anthropogenic climate change

The biological pump of the future ocean will likely change in strength in response to warming and ocean acidification associated with anthropogenic increases in CO₂ in the atmosphere and the ocean. However, the directions of change are difficult to predict. A substantial but undetermined portion (between a fourth and half) of the anthropogenic CO₂ added to the atmosphere during the last two centuries has been taken up by the ocean (Le Quéré et al., 2010; Sabine and Tanhua, 2010; Sabine et al., 2004). The remaining CO₂ in the atmosphere contributes to warming of both the atmosphere and the ocean. Possible effects of anthropogenic global warming on the ocean's biological pump (Fig. 2) are uncertain (Riebesell et al., 2009; Passow and Carlson, 2012; Poloczanska et al., 2013; Tyrrell, 2011), and may relate to separate or interacting effects of increasing temperatures (Barnett et al., 2005; Lyman et al., 2010; Sarmento et al., 2010; Wohlers et al., 2009) and ocean acidification due to increasing amounts of dissolved CO₂ (Fig. 3) being converted to carbonic acid (Doney et al., 2009; Dore et al., 2009; Fabry et al., 2008; Feely et al., 2004; Hofmann et al., 2010; Orr et al., 2005; Tyrrell, 2008). Various perturbations of the biological pump will differ in terms of amplifying or dampening processes, with different sensitivities, strengths, and durations of effects (Riebesell et al., 2009).

Ocean warming is expected to increase stratification of the ocean's surface layer, with reduced nutrient input from below. This may lead to decreased primary productivity and reduction of the export flux through the biological pump, particularly in already-stratified waters of the tropics and subtropics (Behrenfeld et al., 2006; Bopp et al., 2001; Boyce et al., 2010; Doney, 2006; Huisman et al., 2006; Matear and Hirst, 1999; Norris et al., 2013; Sarmiento et al., 1998, 2004; Siegel and Franz, 2010; Yool et al., 2013). Decreases in nutrient supply due to increased stratification may also prompt shifts in phytoplankton community composition from dominance by diatoms to coccolithophorids (Cermeño et al., 2008), or from large diatoms to small microflagellates and cyanobacteria (Falkowski and Oliver, 2007), thereby increasing the length and decreasing the trophic efficiency of marine food chains (Riebesell et al., 2009). There have been long-term shifts toward cyanobacteria with increasing stratification in the North Atlantic (Lomas et al., 2010) and North Pacific (Karl et al., 2001a) subtropical gyres. Emerson et al. (2001) noted that there have been increases in the proportion of nitrogen supplied to the euphotic zone by nitrogen fixation over the last two decades at the HOT station in the North Pacific subtropical gyre. This has resulted in increases in strength of the biological pump over that expected by nitrogen input to the euphotic zone by ocean circulation. Simulations suggest that expected warming by the end of the 21st century will increase the abundance, and expand the biogeographic distributions of the picoplanktonic cyanobacteria *Prochlorococcus* and *Synechococcus* (Flombaum et al., 2013). Increased stratification may also retain more phytoplankton in sunlit waters of the upper mixed layer, thereby increasing primary production by reducing vertical mixing of phytoplankton into deeper darker layers of the water column, particularly in deeply-mixed waters at high latitudes (Riebesell et al., 2009). Warming of the upper ocean may also increase storm frequency and intensity, promoting pulsed delivery of nutrients into the euphotic zone, with increased primary production (Peters, 2008).

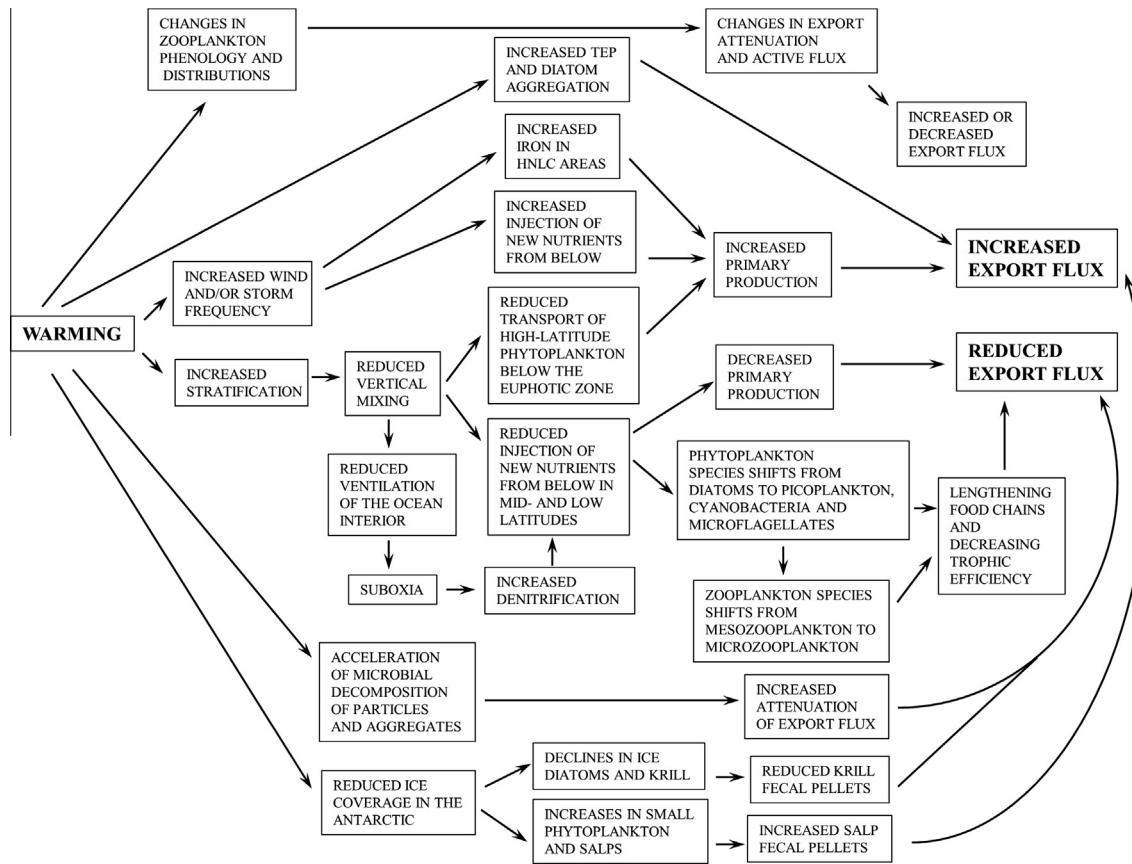


Fig. 2. Potential changes in export flux through the biological pump caused by anthropogenic warming of the ocean. For details and references, please see Section 'The biological pump and anthropogenic climate change'.

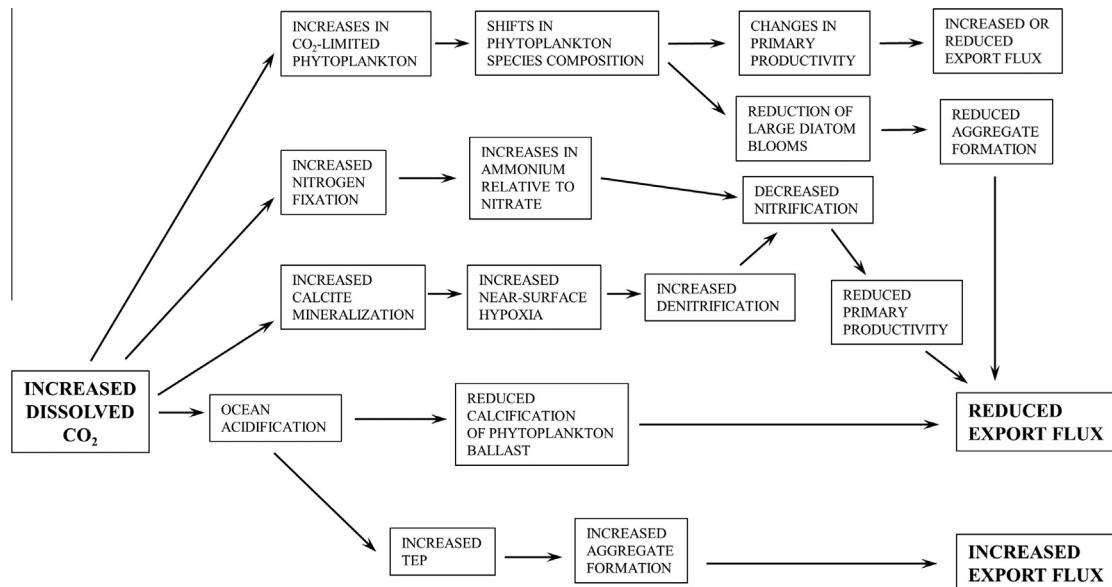


Fig. 3. Potential changes in export flux through the biological pump caused by anthropogenic increases in dissolved CO₂ in the ocean. For details and references, please see Section 'The biological pump and anthropogenic climate change'.

An alternative to the view that stratification will promote the replacement of diatoms by smaller phytoplankton, reducing carbon productivity and export, has been presented by Kemp and Villareal (2013). These authors noted that some diatoms have adaptations to stratified waters, including ability to grow in low

light at deep chlorophyll maxima, vertical migrations between deep nutriclines and illuminated surface depths, and symbioses with nitrogen-fixing cyanobacteria. These strategies promote maintenance of diatom seed populations, which can take advantage of mixing events and bloom, even in oligotrophic subtropical

oceanic waters. Aggregations of such diatoms can enhance export flux to depth. Indeed, Dore et al. (2008) have recorded repeated summer blooms of diatoms and nitrogen-fixing cyanobacteria, with enhanced pulses of export flux, under strongly-stratified and chronically nutrient-depleted conditions in the North Pacific Subtropical Gyre. There is also evidence for diatom blooms in stratified waters in laminated sediments from the Mediterranean during the Cretaceous, and in other “palaeo-sediment trap” records in laminated sediments. Thus, Kemp and Villareal (2013) suggested that rather than decrease as widely predicted, diatom production and export may actually increase with increased stratification. This could potentially act as a negative feedback to global warming by enhancing the biological pump.

Ocean warming also causes changes in biological communities, which can be reflected in the biological pump. Warming accelerates rates of biological processes such as heterotrophic microbial decomposition, which could reduce the effectiveness of export to depth by increasing near-surface attenuation of the biological pump (Riebesell et al., 2009; Wohlers et al., 2009). Warming could also convert surface pelagic ecosystems from those dominated by diatoms and larger zooplankton to those dominated by picoplankton and microzooplankton, thereby reducing the export of particulate detrital food to depth, with subsequent decreases in the abundance, species diversity, body size and taxonomic composition of abyssal benthic animal assemblages (Smith et al., 2008b). Several models have predicted future decreases in global ocean primary productivity and export of POC with continued warming of the ocean (Manizza et al., 2010; Steinacher et al., 2010). Warming may also decrease biological drawdown of DIC in the surface layer, enhancing accumulation of DOC, relative to POC, thereby leading to reduced export flux of POC through the biological pump (López-Urrutia et al., 2006; Harris et al., 2006; Wohlers et al., 2009).

Ocean warming and stratification may affect the remineralization depth at which carbon in sinking particles is converted back to CO₂ (Kwon et al., 2009). Simulations suggest that shoaling of the remineralization depth by warming-induced stratification could redistribute carbon in deeper waters toward the surface, thereby increasing transfer of carbon from the ocean to the atmosphere, further increasing greenhouse warming (Kwon et al., 2009).

Reductions in sea ice coverage in polar regions may change biological communities and the biological pump. Antarctic krill (*Euphausia superba*) have declined by an order-of-magnitude in abundance since 1950 in the southwest Atlantic sector near the Antarctic Peninsula, and krill are being replaced by salps (*Salpa thompsoni*) in many areas (Loeb et al., 1997; Atkinson et al., 2004). Abundance of krill is positively correlated with recruitment from the previous spawning season, which is positively correlated with extensive sea ice during the previous year (Loeb et al., 1997). Conversely, salp abundance is negatively correlated with extensive sea ice. There has been a decreased frequency of winters with extensive sea-ice coverage over the last five decades (Loeb et al., 1997). Sea-ice algae, primarily diatoms, are an important winter food for krill, contributing to adult spawning in spring, and survival of larvae in winter (Atkinson et al., 2004). Krill recruitment is also enhanced by having abundant summer food, primarily diatoms. Summer levels of surface chlorophyll *a*, which are 63% of annually integrated chlorophyll *a*, have declined by 12% near the western Antarctic Peninsula over the last three decades (Montes-Hugo et al., 2009). These declines in chlorophyll appear correlated with concurrent declines in sea-ice coverage. Thus, the decreases in krill and phytoplankton, and increases in salps, all appear to be related to declines in sea ice. In addition, the decreases in phytoplankton are associated with shifts in the phytoplankton community from large cells, such as diatoms that are important food for krill, to small cells that are efficiently grazed by salps (Schofield et al.,

2010). Warming-related declines in sea ice and larger phytoplankton, and replacement of krill by salps can all affect the biological pump. During extensive salp blooms, more of the primary production will be consumed by salps, which produce large fast-sinking fecal pellets that enhance export flux (Loeb et al., 1997). This would reduce the amounts of primary production that are channeled into krill, which consume and fragment phytoplankton chains and aggregates, and form the forage base for higher pelagic consumers from penguins to marine mammals (Schofield et al., 2010). Indeed, these reductions in krill abundance and sea-ice extent have been associated with shifts in abundance or distribution patterns for several Antarctic predators, including Adélie penguins, crabeater seals, Gentoo penguins, and fur seals (Doney et al., 2012; Ducklow et al., 2007). Declines in export flux to the benthos have also been associated with increases in temperature and reductions in sea ice coverage in the northern Bering Sea (Grebmeier, 2012; Grebmeier et al., 2006).

Warming may also enhance formation of marine snow and other organic aggregates. Piontek et al. (2009) found enhanced aggregation of diatoms at higher temperatures, likely related to increased concentrations of TEP at higher temperatures. However, elevated temperatures also stimulated increases in bacteria growth and biomass, leading to more rapid aggregate degradation. Thus, higher temperatures increased both aggregate formation and degradation, which would have effects in both strengthening and weakening the biological pump. Increased temperatures, levels of CO₂ and ocean acidification can increase TEP production (Engel et al., 2004), possibly leading to increased aggregation and faster sedimentation rates (Riebesell et al., 2007). Such strengthening of the biological pump at higher concentrations of CO₂ and TEP would provide a negative feedback on increasing levels of atmospheric CO₂, and may have already mitigated approximately 10% of the additional CO₂ added to the atmosphere due to anthropogenic activities in the last two centuries (Arrigo, 2007; Riebesell et al., 2007). Increased production of TEP was found in the experiments of Engel et al. (2004), but not in those of Schulz et al. (2008) and Egge et al. (2009). However, ocean acidification enhanced POC export to depth in the experiments of Schulz et al. (2008) and Egge et al. (2009).

Ocean acidification may reduce calcification of plankton that contain CaCO₃ as mineral ballast, such as coccolithophorids, thereby reducing the export flux and weakening the biological pump (Bach et al., 2012a, 2012b; Beaufort et al., 2011; Berger et al., 2014; De Jesus Mendes and Thomsen, 2012; Hofmann and Schellnhuber, 2009; Hutchins, 2011; Meier et al., 2014; Riebesell et al., 2000). Reduction of the export flux of calcareous plankton may lead to oxidation of calcareous-ballasted plankton in shallower near-surface waters, which because of warmer temperatures contain less dissolved oxygen, leading to expansion of hypoxic waters (Hofmann and Schellnhuber, 2009; Oschlies et al., 2008). Such expansion of hypoxic areas in the ocean may increase denitrification (Deutsch and Weber, 2012) and decrease nitrification in oceanic areas (Beman et al., 2011). Reduced calcification due to ocean acidification may lead to “ocean carbonation” wherein dissolved CO₂ increases in seawater, to the benefit of some groups of photosynthetic phytoplankton that are relatively inefficient in CO₂ acquisition (Riebesell et al., 2009).

Ocean acidification is also expected to alter cycles of major nutrients, particularly nitrogen (Hutchins et al., 2009). Expected changes include increases in nitrogen fixation by cyanobacteria (Boyd et al., 2010; Hutchins et al., 2009), increased denitrification with expansion of suboxic water and loss of fixed nitrogen from the ocean (Oschlies et al., 2008), and decreased nitrification (Beman et al., 2011; Yool et al., 2007). Such changes in nutrients would likely favor some types of phytoplankton such as cyanobacteria and picoplankton (Boyd et al., 2010; Hutchins et al., 2009), to

the detriment of others such as diatoms, which are important components of the biological pump.

Expected changes in ocean warming and acidification will simultaneously alter temperature, carbonate, stratification, mixing, nutrient and biological regimes in the ocean in ways that will be different in different regions of the ocean (Passow and Carlson, 2012; Riebesell et al., 2009; Rost et al., 2008). These combinations of concurrent multiple effects, including changes in temperature, light intensity, nutrients, CO₂ levels, ocean acidification, and changes in the composition of plankton assemblages, complicate predictions based on individual parameters (Boyd and Hutchins, 2012; Boyd et al., 2010; Bopp et al., 2013; Hutchins et al., 2009; Legendre and Rivkin, 2005). Thus, oceanographers are currently unable to accurately predict whether the biological pump will strengthen or weaken over the next century. Numerous contrasting results in the literature are due to comparisons of different geographical areas, ecosystems, conditions, and organisms. The biological pump is subject to variations in multiple interacting parameters and synergistic effects, all of which can affect export and sequestration flux and flux attenuation. Quantifying the efficiency of the biological pump, both currently and in the future, is a prerequisite for constructing realistic global carbon models (Usbeck et al., 2003). However, in recent models of projected effects of ocean warming and acidification on the biological pump (Kwon et al., 2011; Tagliabue et al., 2011), large uncertainties remain as to how the epipelagic production system will respond to such changes. Some recent simulations (Fung et al., 2005; Henson et al., 2013; Laufkötter et al., 2013; Le Quéré et al., 2007; Lovenduski et al., 2007; Wetzel et al., 2005; Wang and Moore, 2012) suggest that global primary productivity and carbon export to depth by the biological pump have already decreased in recent decades, and that warming of the ocean acts to increase atmospheric CO₂ levels, thereby amplifying atmospheric and ocean warming.

Conclusions

The biological pump is one of the most important processes on the planet. It is a critical component in the removal of CO₂ from the atmosphere and the sequestration of CO₂ in the deep sea. As anthropogenic CO₂ in the atmosphere continues to increase, the resulting warming is expected to decrease the ability of the biological pump to scrub CO₂ from the atmosphere. Vast portions of the global ocean are already chronically depleted in nutrients that are required for near-surface photosynthesis due to thermal stratification. Further warming is expected to exacerbate stratification, reducing nutrient injection to the euphotic zone from below, reducing primary productivity, and export of carbon to depth. The relative contributions of zooplankton fecal pellets, marine snow and phytoplankton to carbon export are all important and highly-variable in various areas of today's ocean, and predicting how global warming will change these contributions is challenging. Thus, a better understanding of the efficiency and dynamics of the present biological pump is critical to predicting future effects of global warming on the ocean.

Although we appear to understand the basics of how the biological pump functions, we are far from realistically quantifying it. There are still major discrepancies between estimates of export to, and utilization of organic carbon in the deep sea. In a review of major results of the HOT, BATS, and CARIACO time-series programs, Church et al. (2013) noted that "geochemical mass balances appear as much as 4-fold greater than predicted based on sediment trap estimates of carbon export" and that "Such discrepancies provide sobering reminders that there remain a number of unresolved issues central to our understanding of ocean ecosystem functioning."

Shipboard multi-decadal ocean time-series are critical to our understanding of the connections between variability in climate and ocean ecology and biogeochemistry (Church et al., 2013). Such time-series are expensive and labor-intensive, but they provide information that cannot be otherwise obtained. Such time-series programs should be continued and expanded. Otherwise we will continue to have inadequate understanding of the contemporary functioning of the largest habitat on the planet, and impossibility of predicting future changes in it.

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