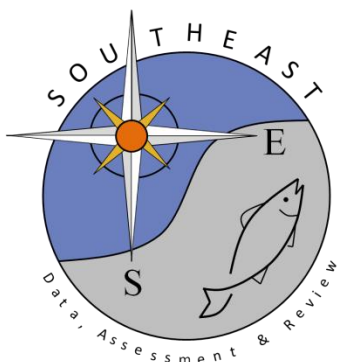


Zooplankton and the Ocean Carbon Cycle

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Zooplankton and the Ocean Carbon Cycle

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Keywords

metabolism, food web, efficiency, biological pump, climate change

Abstract

Marine zooplankton comprise a phylogenetically and functionally diverse assemblage of protistan and metazoan consumers that occupy multiple trophic levels in pelagic food webs. Within this complex network, carbon flows via alternative zooplankton pathways drive temporal and spatial variability in production-grazing coupling, nutrient cycling, export, and transfer efficiency to higher trophic levels. We explore current knowledge of the processing of zooplankton food ingestion by absorption, egestion, respiration, excretion, and growth (production) processes. On a global scale, carbon fluxes are reasonably constrained by the grazing impact of microzooplankton and the respiratory requirements of mesozooplankton but are sensitive to uncertainties in trophic structure. The relative importance, combined magnitude, and efficiency of export mechanisms (mucous feeding webs, fecal pellets, molts, carcasses, and vertical migrations) likewise reflect regional variability in community structure. Climate change is expected to broadly alter carbon cycling by zooplankton and to have direct impacts on key species.

Biological pump:

the suite of biological processes that mediate transport of carbon from the upper ocean to depth

1. INTRODUCTION

The pelagic food web plays a central role in regulating the exchange of CO₂ between the atmosphere and the surface ocean, as well as the transfer of organic carbon into the deep sea. Within this food web, zooplankton serve both as trophic links between primary producers and higher trophic levels (such as fish) and as recyclers that transform particulate carbon and nutrients into dissolved pools. The enormous diversity in zooplankton taxa, life history, size, trophic ecology, and physiology makes for fascinating study of their roles in food webs and biogeochemical cycles. These roles, however, are represented simplistically in ecosystem and biogeochemical models, which can be sensitive to small changes in zooplankton physiological functions and rates (Mitra et al. 2014) and improved by adding behaviors such as food selectivity (Sailley et al. 2013). As climate change and other stressors affect zooplankton abundance, biogeography, size structure, and life cycles (Beaugrand et al. 2002, Richardson 2008, Mackas et al. 2012), it becomes increasingly important to understand the various roles of zooplankton in carbon transformations and to predict future changes.

This review describes the fundamental and multifaceted roles that zooplankton (both protistan and metazoan; see sidebar Classification of Planktonic Consumers) play in the cycling and export of carbon in the ocean (**Figure 1**). We begin with their roles as consumers and follow the path of ingested carbon as it is absorbed, egested, metabolized, and made available to higher trophic levels through growth and reproduction. This leads to an analysis of food-web fluxes based on current global constraints on zooplankton feeding and energetics. We then progress to the roles of zooplankton in vertical export and the biological pump, and conclude with long-term and future changes in zooplankton carbon cycling. Throughout, we explore these processes and roles across regions and taxa and consider a range of observational, experimental, and modeling studies.

2. FEEDING RELATIONSHIPS AND IMPACTS

Within microzooplankton, the >5- μ m flagellates (technically nano-sized; Sieburth et al. 1978) are major consumers of prokaryote populations, including heterotrophic bacteria, archaea, and the cyanobacteria *Prochlorococcus* and *Synechococcus* spp. (Fenchel 1982, Calbet & Landry 1999). Larger microzooplankton, including ciliates and dinoflagellates, feed generally on protists of intermediate size (Sherr & Sherr 2002), although some large dinoflagellates are notable for their ability

CLASSIFICATION OF PLANKTONIC CONSUMERS

Planktonic consumers can be divided into two operationally defined size classes, the micro- and mesozooplankton, depending on whether they pass through or are retained on 200- μ m mesh screening. The microzooplankton size class (<200 μ m) is functionally dominated by protistan (unicellular eukaryote) consumers but also includes smaller juvenile stages of metazooplankton species (Paffenhöfer 1998, Quevedo & Anadón 2000). The mesozooplankton size class (0.2–20 mm) consists mainly of true animals but also includes large protists, such as pelagic foraminifera and radiolaria (Stoecker et al. 1996). The term macrozooplankton is also commonly used for larger planktonic animals (>20 mm), such as large gelatinous zooplankton, but here, for convenience, we include them in the mesozooplankton. Both the micro- and mesozooplankton size classes are functionally diverse assemblages comprising multiple trophic levels with complex feeding relationships (Sanders & Wickham 1993, Verity & Smetacek 1996, Vargas et al. 2007).

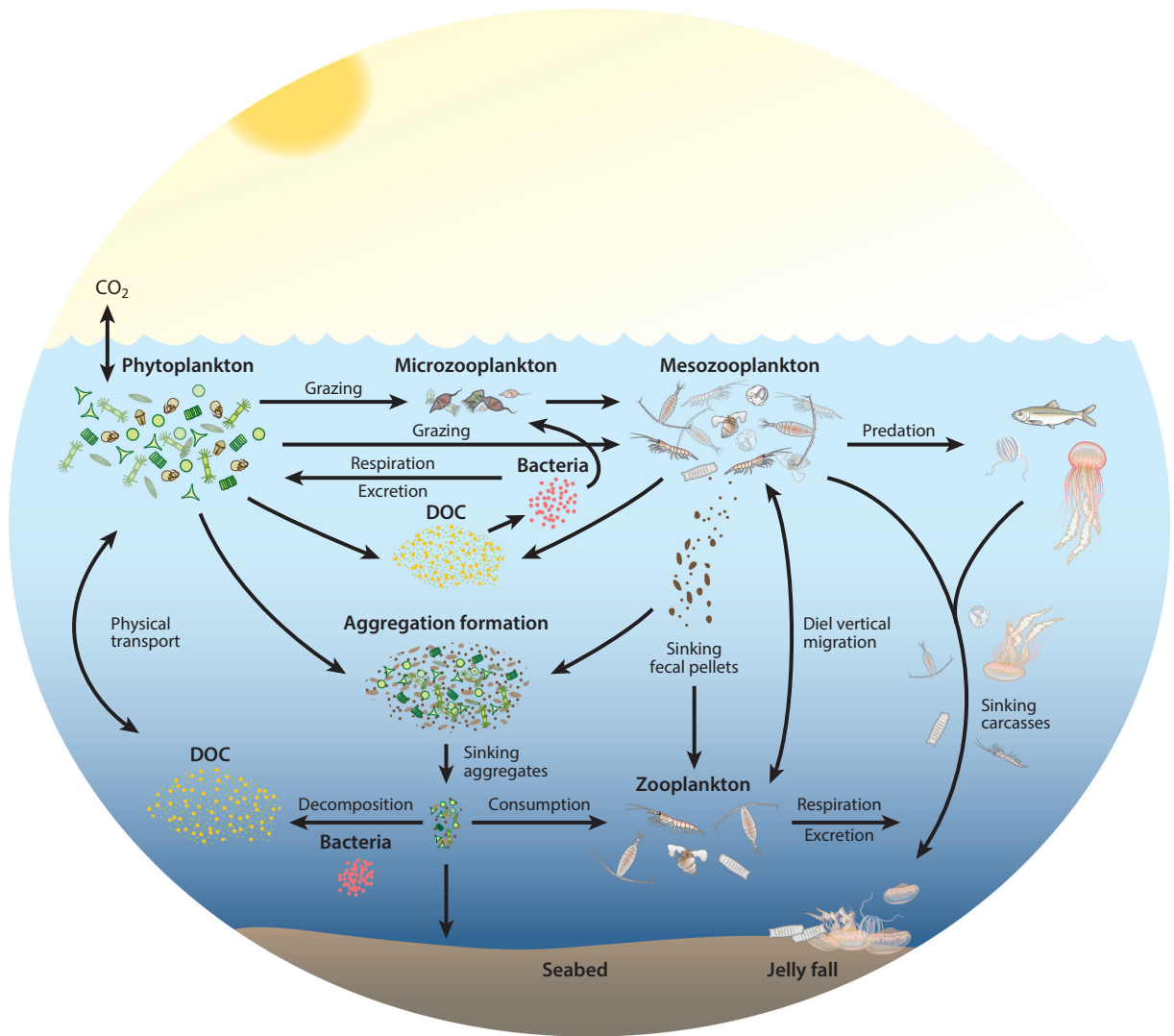


Figure 1

Pathways of cycling and export of carbon by zooplankton in the ocean. Phytoplankton take up CO_2 via photosynthesis in the euphotic zone and are consumed by herbivorous micro- and mesozooplankton. In the multistep food web, where much of their carbon is respired, microzooplankton are also the major prey of mesozooplankton. Phytoplankton particulate organic carbon (POC) is respired by zooplankton as CO_2 and excreted as dissolved organic carbon (DOC), which is used by phytoplankton or bacteria to fuel the microbial loop. Mesozooplankton POC is transferred further up the food web to higher-level predators. Mesozooplankton and their predators egest sinking fecal pellets, which can form into larger sinking aggregates. Diel vertical migrators feed in surface waters at night and metabolize the food they ingested in the mesopelagic zone during the day; seasonal vertical migrations also occur. Zooplankton and bacteria in the mesopelagic zone ingest and metabolize sinking POC, leading to attenuation of sinking POC. Carcasses of dead zooplankton include bloom-forming gelatinous zooplankton that can give rise to rapidly sinking jelly falls to the deep benthos. Advection below the mixed layer of DOC produced by phyto- and zooplankton in surface waters is also an important export mechanism; this advection, the sinking of particles, and vertical migration comprise the biological pump. Adapted from previous representations by D.K. Steinberg incorporated into a Joint Global Ocean Flux Study cartoon, Lebrato & Jones (2011), and Steinberg (2017).

to selectively capture and consume large diatoms (Strom & Buskey 1993, Hansen et al. 1994). Trophic interactions within the microbial component of food webs are further complicated by widespread mixotrophy, in which pigmented, photosynthetically capable cells also possess the ability to consume prey (Thingstad et al. 1996, Stoecker 1998, Stoecker et al. 2009, Flynn et al. 2013).

Copepods typically make up 70–90% of mesozooplankton abundance (Turner 2004). Most copepods operate as omnivorous suspension feeders that prey broadly on heterotrophic protists, small animals (e.g., eggs and nauplii), and likely detritus, in addition to phytoplankton (Sherr et al. 1986, Stoecker & Capuzzo 1990, Calbet & Saiz 2005). As the major consumers of microzooplankton, mesozooplankton represent the main utilization pathway of the secondary production generated by smaller consumers that feed directly on phytoplankton. In addition, the diets of mesozooplankton that feed by mucous nets, such as pelagic tunicates (appendicularians, salps, and doliolids) and pteropods, can include prey as small as bacterioplankton that broadly overlap the size range exploited by microzooplankton (Scheinberg et al. 2005, Sutherland et al. 2010). At the same time, however, a diverse assemblage of organisms that use active raptorial prey hunting (predatory crustaceans), ambush (chaetognaths), or entangling (ctenophores and medusae) capture strategies function primarily as carnivores. Dietary breadth can thus be as different within the mesozooplankton as it is between meso- and microzooplankton. Carbon and energy flows within the mesozooplankton are further complicated by changes in dietary breadth during species development and by large size differences between early stages and adults, which blurs the trophic separation of predators and prey, leading to unstructured food webs and convoluted energy flows (Isaacs 1973, Landry 2002).

Although existing data are insufficient to assess trophic flows along the diverse pathways of plankton food webs, several attempts have been made to derive global estimates of the feeding impacts associated with major zooplankton size classes. Based on results from dilution experiments, for example, Calbet & Landry (2004) concluded that microzooplankton consume 67% of primary production (PP), on average, as direct feeding on phytoplankton, establishing their role as dominant primary consumers in both coastal and open-ocean systems. Estimates of mesozooplankton herbivory, determined from the combined results of experimental and gut fluorescence studies in natural systems, range from 10% (in high-productivity regions) to 40% (in low-productivity regions) (Calbet 2001). Although the proportion of production consumed by mesozooplankton varies inversely with system productivity, mean weight-specific grazing estimates are more than threefold higher (20% versus 6% of biomass per day) when production exceeds $1 \text{ g C m}^{-2} \text{ d}^{-1}$ compared with when it is less than $0.25 \text{ g C m}^{-2} \text{ d}^{-1}$ (Calbet 2001).

Schmoker et al. (2013) extended microzooplankton grazing assessments to major biogeographical provinces of the ocean, which were combined with estimates of mesozooplankton feeding on phytoplankton and ciliates to create a global budget of carbon fluxes for epipelagic food webs. The median regional estimates for microzooplankton grazing in this analysis ranged from 49% to 77% of PP, with a global value of 62% based on the province-weighted productivity estimates of Longhurst et al. (1995). For a total 50 Gt C y^{-1} of PP, 31 Gt C y^{-1} (62%) was ascribed to grazing by microzooplankton, 6 Gt C y^{-1} (12%) to consumption by mesozooplankton (Calbet 2001), and 3 Gt C y^{-1} (6%) to viral lysis, leaving 10 Gt C y^{-1} (20%) of ungrazed production for direct sinking as algal aggregates. Mesozooplankton receive an additional dietary supplement of 5.6 Gt C y^{-1} from predation on microzooplankton, which is double the estimate of mesozooplankton feeding on ciliates (Calbet & Saiz 2005), to account for consumption of heterotrophic dinoflagellates and other nonciliate microzooplankton prey. We revisit this food-web flux analysis further below with additional constraints and perspectives (see Section 6.1).

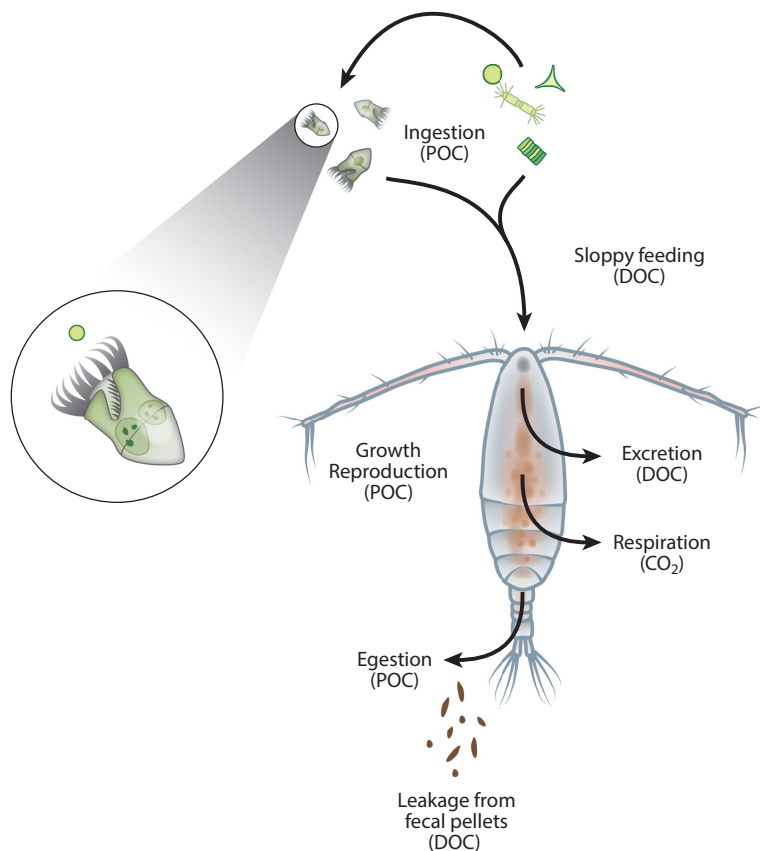


Figure 2

Carbon consumption and metabolism by zooplankton. Prey (phytoplankton or other zooplankton) particulate organic carbon (POC) is consumed by zooplankton. Because of sloppy feeding (by metazoa), some of the dissolved organic carbon (DOC) in the prey is lost to the surrounding water while the rest of the prey is ingested. Some of the POC that is ingested is absorbed across the digestive vacuoles (protists; see magnified inset at left) or the gut walls (metazoa) of consumers, the proportion of which is termed absorption efficiency. Carbon that is not absorbed is egested as fecal pellets, including mini-pellets egested by protists, which may subsequently leach DOC. Of the carbon that is absorbed, a portion is respired as CO_2 , and the rest is used for the animal's growth and reproduction (secondary production). Adapted from Møller et al. (2003) and Saba et al. (2009).

3. ABSORPTION EFFICIENCY AND EGESTION

Absorption efficiency (AE), the proportion of ingested food absorbed across the digestive vacuoles of protistan consumers or the gut walls of metazoan consumers, determines the availability of organic constituents to meet zooplankton requirements for metabolism and growth (**Figure 2**). (AE is also commonly called assimilation efficiency, although assimilation efficiency was originally meant to refer to the portion of nutrition that is available for organism growth and reproduction; see Bochkansky et al. 1999.) The same process also determines the organic content of the unabsorbed fraction that zooplankton return to the environment as egesta to be utilized or remineralized within the euphotic zone or exported to depth as packaged fecal pellets.

Remineralization: transformation of (particulate or dissolved) organic matter into its inorganic constituents

Carbon export efficiency:

the amount of organic carbon exported from the surface-ocean layer divided by the amount produced by photosynthesis

AE is usually assumed to be a constant 70% in most marine ecosystem models or bioenergetic calculations, and estimates of this approximate magnitude are well documented in field and laboratory studies. For example, Bochdansky et al. (1999) found mean AEs of 74% and 67%, respectively, for a copepod mixture (*Calanus* spp.) and a large appendicularian (*Oikopleura vanboeffeni*). Similarly, Madin & Purcell (1992) derived AE estimates of 61% for carbon and 71% for nitrogen for the salp *Cyclosalpa bakeri* feeding on natural particulates in the subarctic Pacific. Other studies, however, have shown substantial AE variability with food nutritional quality. Purcell (1983), for instance, measured uniformly high values of 87–94% for carbon and 90–96% for nitrogen for four genera of siphonophores, highlighting the fact that carnivores can digest their prey (which closely resemble their own protein-rich body composition) more efficiently than herbivores can. This also illustrates the general result that nitrogen is typically absorbed more efficiently than carbon, which leads to more efficient cycling of nitrogen in the upper ocean as well as enhanced carbon export efficiency by the biological pump. For the copepod *Acartia tonsa*, Besiktepe & Dam (2002) determined carbon-based AEs ranging from <10% to >95% for various types and concentrations of protistan prey. Thor et al. (2007) also reported low carbon AEs of 37–49% for the same copepod feeding on unialgal cultures, demonstrating a connection to nutritional quality when a mixture of cultures with complementary fatty acids led to enhanced AE (61%) and higher egg production and hatching success. In addition, certain phytoplankton, such as the cyanobacteria *Synechococcus* spp. and some diatoms, have the ability to resist digestion and pass intact through zooplankton guts (Silver & Bruland 1981, Johnson et al. 1982, Bathmann & Liebezeit 1986). Differential digestibility may thus contribute to the observed disproportionate presence of some cell types, and their DNA, in sediment-trap and deep-sea samples relative to their proportional presence in the overlying euphotic zone (Amacher et al. 2013).

As might be expected from variable AEs, the nutritional quality and sinking characteristics of the egesta produced by zooplankton can vary greatly depending on the feeding environment. Under controlled conditions, experimental studies have documented food type and concentration effects on fecal pellet production rates, pellet volumes, and density, the latter reflecting variability in compactness and mineral ballasting (Besiktepe & Dam 2002). More importantly, high variability in fecal pellet characteristics is evident under natural field conditions, as observed in a notably detailed study of Antarctic krill, *Euphausia superba* (Atkinson et al. 2012). Among the characteristics measured, the ratio of carbon to dry weight varied by a factor of 75; the ratio of carbon to nitrogen varied by almost a factor of 3; and the pellet diameters and sinking rates varied by factors of 7.5 and 45, respectively. When feeding rates were low, digestion slowed, AE increased, and the pellets were smaller and denser and sank rapidly. When feeding rates were high, digestive processing was less complete, resulting in larger pellets with higher organic content, slower sinking, and greater potential for disaggregation or remineralization in the upper ocean. Even for a single zooplankton species, therefore, factors that regulate the digestive processing of their ingested food can lead to quite different outcomes with regard to the flow of carbon, nutrients, and energy within and between the organism and its environment.

4. METABOLISM

4.1. Respiration

Respiration is a central process governing the balance of organic matter production (photosynthesis) and loss (respiration or remineralization) in the ocean. Estimated global, full-ocean-depth-integrated mesozooplankton respiration accounts for 13 Gt C y⁻¹, equivalent to 17–32% of global PP (based on 41–77 Gt C y⁻¹ of global PP; del Giorgio & Duarte 2002, Hernández-León & Ikeda 2005a). At the regional scale, detailed zooplankton community analysis for the Southern

Ocean provides an estimate of $\sim 0.6 \text{ Gt C y}^{-1}$, equivalent to 22–31% of the region's PP of 1.95–2.7 Gt C y^{-1} (Mayzaud & Pakhomov 2014). Thus, zooplankton respiration is a major loss term for organic carbon.

Typically, approximately 50% of the carbon absorption by zooplankton is respired (**Figure 2**), but this proportion is influenced by many factors. The two primary factors are temperature and body mass, which have been used extensively in multiple regression models to predict respiration and excretion rates of marine zooplankton (e.g., Ikeda et al. 2001, Ikeda 2014). Q_{10} , the factor by which metabolic rates increase for a 10°C increase in temperature, averages 1.9 for a range of meso- and macrozooplankton taxa (Ikeda 2014). Although respiration rates increase with animal body mass, weight-specific respiration decreases with body mass. Generally, the combined effects of temperature and body mass result in tropical and subtropical zooplankton with higher weight-specific respiration rates owing to their smaller size and warmer habitat temperature compared with the larger body size of polar zooplankton (Hernández-León & Ikeda 2005a; but see Isla et al. 2004). Analogous changes in body mass (increase) and temperature (decrease) with depth lead to a decrease in weight-specific respiration rates with increasing depth (Teuber et al. 2013).

Thermal thresholds and the balance of energetic gains and losses in zooplankton are suggested to be valuable predictors of zooplankton responses to climate change. For a similar rise in temperature, losses of metabolic carbon via respiration tend to be higher than energetic gains from ingestion of particulate organic carbon (POC), as demonstrated for the arctic copepod *Calanus glacialis* (Alcaraz et al. 2014). Warming beyond temperatures that increase this metabolic imbalance may lead to a tipping point for a major shift in pelagic ecosystem structure (Alcaraz et al. 2014) and thus also in carbon cycling.

Other biological and physical factors that affect respiration include food concentration, pressure, light, pH, and oxygen (reviewed in Hernández-León & Ikeda 2005b); locomotory activity (Seibel & Drazen 2007); and developmental stage (Almeda et al. 2011). Oxygen has been of considerable recent interest because of increasing coastal hypoxia and expansion of oxygen minimum zones (OMZs) and is discussed further in Section 8. The relative importance of factors causing variation in respiration is still under some debate (e.g., Seibel & Drazen 2007), and conversion of zooplankton O_2 consumption rates to respiratory carbon losses as CO_2 is subject to some variation in the conversion (respiratory quotient) factor used as well (see sidebar Converting Zooplankton O_2 Consumption Rates to Respiratory Carbon Losses as CO_2), both of which could affect carbon flux estimates.

CONVERTING ZOOPLANKTON O_2 CONSUMPTION RATES TO RESPIRATORY CARBON LOSSES AS CO_2

Respiration in zooplankton is often measured by O_2 consumption rather than by direct CO_2 production. O_2 consumption rates are converted to respiratory carbon losses as CO_2 using the appropriate stoichiometry and a respiratory quotient (RQ, the molar ratio of CO_2 produced to O_2 consumed) as follows:

$$\mu\text{g C utilized d}^{-1} = \mu\text{L O}_2 \text{ utilized d}^{-1} \times (12/22.4) \times \text{RQ},$$

where 12/22.4 is the mass (12 g) of carbon in 1 mol (22.4 L) of CO_2 . The RQ depends on the substrate being metabolized (protein, carbohydrate, lipid, or nucleic acid), with protein metabolism ($\text{RQ} = 0.97$) most widely assumed because NH_3 , the end product of protein metabolism, is the primary nitrogenous waste product of marine zooplankton (Hernández-León & Ikeda 2005b). Mayzaud et al. (2005) reported RQs for a number of mesozooplankton taxa and showed RQ ranges between 0.61 and 1.62.

Dissolved organic matter (DOM):

the fraction of organic matter dissolved in water, typically operationally defined as passing through a filter with a 0.45- μm pore size

Coprophagy:

consumption of fecal pellets

4.2. Excretion or Release of Dissolved Organic Carbon

Zooplankton-mediated release of dissolved organic matter (DOM) is one of the principal mechanisms controlling the quantity, composition, and cycling of DOM in the sea (Carlson & Hansell 2014). Release of DOM by zooplankton supports bacterial growth, fueling the microbial loop (Peduzzi & Herndl 1992, Hansson & Norrman 1995, Hygum et al. 1997). The DOM released can be highly labile, as evidenced by its rapid utilization by bacteria (Condon et al. 2011). Zooplankton may release dissolved organic carbon (DOC) and other DOM via sloppy feeding (physical breakage of the food source), excretion, egestion of dissolved digestive products (from metazoan guts or protozoan food vacuoles), and leaching from fecal pellets (Lampert 1978, Strom et al. 1997, Møller 2007) (**Figure 2**). Although excretion is the only one of these processes that results from the metabolism of absorbed carbon (**Figure 2**), we include all pathways of DOC release here, as differentiating among them experimentally can be challenging. Studies to date have suggested that excretion and sloppy feeding are the dominant modes of DOC release of crustacean zooplankton, with fecal pellet leaching playing a relatively minor role. For example, Saba et al. (2011) found that excretion and sloppy feeding constituted 80% and 20% of total DOC released, respectively, whereas any DOC release from fecal pellet leaching was undetectable. Protozoan grazers release DOC primarily through excretion and egestion (Strom et al. 1997, Nagata 2000), and gelatinous zooplankton can release DOC via production of carbon-rich colloidal mucus in addition to the other mechanisms above (Hansson & Norrman 1995; Condon et al. 2009, 2011). Although values range widely, on the order of 10–30% of POC ingested by protozoan and metazoan zooplankton is released as DOC, with zooplankton DOC release comparable to or exceeding that by phytoplankton extracellular release (e.g., see the reviews Nagata 2000, Carlson 2002, Ruiz-Halpern et al. 2011, and Carlson & Hansell 2014). In addition, the remnants of individual small prey egested from protistan feeding vacuoles will enter the DOC pool as they decompose and solubilize in the euphotic zone.

Prey size and zooplankton diet composition are important controls on DOC release rates. Studies using ^{14}C -labeled phytoplankton have indicated a large range in the fraction of phytoplankton carbon ingested that is released as DO^{14}C via copepod sloppy feeding ($\sim 7\text{--}70\%$) (Copping & Lorenzen 1980; Møller & Nielson 2001; Møller et al. 2003; Møller 2005, 2007). This variability in DOC production is partially a function of the relative sizes of predator and prey. The larger the prey is relative to the copepod, the higher the release caused by sloppy feeding will be; very small prey are ingested whole, with little or no DOC produced (Møller 2005, 2007). Differences in zooplankton diet also affect the magnitude and stoichiometry of DOM released. For example, release rates of DOC and NH_4^+ by the copepod *A. tonsa* were higher for a carnivorous diet of heterotrophic dinoflagellates than for a mixed, omnivorous diet of diatoms and heterotrophic dinoflagellates, despite similar ingestion rates and ratios of carbon to nitrogen in prey between treatments (Saba et al. 2009). Fecal pellets produced by *A. tonsa* fed cryptophytes or dinoflagellates had faster rates of decomposition and DOC release than those fed diatoms (Thor et al. 2003). Leaching of DOC from pellets may occur within minutes of egestion (Møller et al. 2003) and continue for hours or even days (Urban-Rich 1999, Thor et al. 2003), and may be maximized under conditions of high food concentration and quality and during breakage by coprophagy (Carlson & Hansell 2014).

5. GROWTH AND PRODUCTION

There is no standard approach for directly assessing zooplankton growth that can be applied to the whole community or at the scale of ocean PP measurements. However, various methods have been advanced for extrapolating from empirical relationships and general principles to local, regional, or global estimates of zooplankton production.

For microzooplankton, production estimates can be made from measured rates of community grazing using an assumed gross growth efficiency (GGE). Landry & Calbet (2004) argued that 30% (Straile 1997) was a reasonable average carbon GGE estimate for mixed protistan communities over the normal range of ocean conditions because of the low inherent basal metabolic requirements of the organisms in these communities (Fenchel & Finlay 1983) and rapid compositional adjustments to environmental variability (i.e., selection for species and types that can grow optimally at ambient conditions). Thus, the combined grazing impacts on phytoplankton and bacteria (60–75% and 10% of PP, respectively) lead to secondary production estimates of 21–25% of PP for microzooplankton in varying ecosystems (estuarine to oceanic, tropical to polar) (Landry & Calbet 2004). However, total microzooplankton production estimates can even be higher (27–33% of PP) if there are two trophic levels of protistan consumers between phytoplankton and mesozooplankton.

For mesozooplankton, production estimates are more easily approached from derived relationships based on temperature and body size rather than their GGEs, which can be variable and food dependent. Huntley & Lopez (1992) initially explored this idea with a data synthesis that demonstrated a strong temperature dependency of mean instantaneous growth rates of copepod species, derived from developmental times and egg-to-adult biomass ratios. Over a broad tropical-to-polar temperature range of -1.7°C to 30°C , temperature alone accounted for 90% of the variability in growth rate, suggesting that species size differences were inconsequential for estimating productivity from zooplankton biomass estimates. Subsequent studies have nonetheless demonstrated that body weight information improves the predictability of copepod generation times and juvenile growth rates (Hirst & Sheader 1997) as well as the growth rates of broadcast-spawning adults, measured as weight-specific production of egg biomass (Hirst & Lampitt 1998). The resulting empirical relationships thus provide a means for predicting the growth and production of the numerically dominant metazooplankton in marine systems using two easily measured parameters, temperature and size-structured biomass.

Although the applicability of such copepod-based equations to diverse mesozooplankton assemblages has not been rigorously tested, the approach has been used to evaluate zooplankton trophic flows in several regions with the requisite data to put them into an ecological context. In the Arabian Sea, for example, mesozooplankton biomass was estimated to grow at a mean instantaneous rate of 0.12 d^{-1} , implying daily carbon consumption equivalent to approximately 40% of zooplankton biomass and 40% of phytoplankton production (Roman et al. 2000). From similar calculated carbon fluxes for subtropical ocean time-series stations, Roman et al. (2002) found that similar PP supported twice the zooplankton production in the Pacific [5.5% of PP at the Hawaii Ocean Time-series (HOT) site] compared with the Atlantic [2.7% of PP at the Bermuda Atlantic Time-series Study (BATS) site], which the authors ascribed to inefficiencies of trophic coupling or missed event-scale blooms of gelatinous consumers at the Atlantic site.

6. FOOD-WEB CYCLING

While acknowledging that material flows through individual zooplankton vary substantially with taxon, food, and environmental conditions that are not well understood, here we apply the general community-level empirical relationships discussed above (Sections 4 and 5) to an upper-ocean carbon budget on a global scale. Such an analysis allows us to focus on the major trophic pathways involving zooplankton, their structural uncertainties, and the implications of those uncertainties for carbon fluxes within a constrained network of trophic interactions. This section also sets the stage for subsequent considerations of more complex food-web issues (dynamics, mixotrophy) as well as the roles zooplankton play in the ocean's biological pump.

Gross growth efficiency (GGE): the proportion of food ingested by an animal that is converted into growth

Instantaneous growth rate: for exponential growth, the slope of the regression of time versus log-transformed biomass; the unit is per day (d^{-1})

6.1. A Constrained Upper-Ocean Carbon Budget

As done previously by Schmoker et al. (2013), our analysis begins with global estimates of microzooplankton grazing, the largest direct consumption loss for phytoplankton production and the most widely measured. Importantly, however, we add global estimates of mesozooplankton respiration to better constrain their nutritional requirements and feeding impacts. Using the Schmoker et al. (2013) data set with an arctangent transformation of the grazing: growth ratio according to the method described by Calbet & Landry (2004), we derive a mean estimate of 66% of phytoplankton PP consumed by microzooplankton (**Figure 3**), which slightly exceeds the 62% median estimate previously reported but arguably better represents the rarer occurrences where grazing exceeds production. Assuming a mean global PP of 50 Gt C y^{-1} as the scaling basis, microzooplankton herbivory accounts for the utilization of 33.2 Gt C y^{-1} . To this we add 10% of global PP (5 Gt C y^{-1}) as microzooplankton consumption of bacterial secondary production, which has been estimated to be 10–15% of PP on average (Anderson & Ducklow 2001), the excess going to viral lysis. Assuming that microzooplankton GGE is 30% (Straile 1997), the maximum microzooplankton production that could be consumed by mesozooplankton is 11.5 Gt C y^{-1} . This is double the estimate of 5.6 Gt C y^{-1} that Schmoker et al. (2013) determined based on extrapolations of mesozooplankton predation on ciliates by Calbet & Saiz (2005). However, if the transfer of microzooplankton production to mesozooplankton involves two intermediate food-web steps rather than one, then that flux would be reduced by 70%. Thus, the range of $11.5\text{--}3.4 \text{ Gt C y}^{-1}$ shown in **Figure 3** (where the first number is the value for a scenario with one trophic level between phytoplankton and mesozooplankton, and the second is the value for a scenario with two intermediate levels of consumers) reflects uncertainty in the mean trophic structure of the microbial food web.

The global respiratory estimate of 10.4 Gt C y^{-1} for mesozooplankton in the upper 200 m of the oceans (Hernández-León & Ikeda 2005a) is a major constraint on carbon absorption requirements of animals that depend directly on phytoplankton production in the euphotic zone. In this regard, the total global ingestion of mesozooplankton from combined phyto- and microzooplankton in the Schmoker et al. (2013) analysis is 11.5 Gt C y^{-1} , which is equivalent to $\sim 8 \text{ Gt y}^{-1}$ of carbon absorbed (assuming $\text{AE} = 70\%$) and far short of what is needed to satisfy metabolic demands in the absence of any growth. There is consequently a gross inconsistency in the previous budget with respect to global ingestion and respiration estimates for mesozooplankton. Alternatively, if respiratory losses make up 50% of the mesozooplankton energetic budget on average (consistent with $\text{AE} = 70\%$ and $\text{GGE} = 20\%$), the missing ingestion of mesozooplankton not provided by microzooplankton consumption must be $9.3\text{--}17.4 \text{ Gt C y}^{-1}$ (19–35% of PP) for the range of microbial food-web structures (one or two trophic steps) represented in **Figure 3**. These estimates exceed by two- to threefold Calbet's (2001) estimate of 5.5 Gt C y^{-1} for global mesozooplankton herbivory. We note, however, that the mean estimate for that data set was 23% of PP (Calbet 2001) before geometric transformation and regression analysis diminished the impact of the higher grazing results. Consequently, a different interpretation of the same data might suggest higher mesozooplankton herbivory of a magnitude that falls within the range of what we calculate will meet ingestion requirements for metabolism and growth. In addition, Buitenhuis et al. (2010) showed that a model constrained by global biomass data for microzooplankton consistently set rates of mesozooplankton herbivory in the range that we suggest here ($10\text{--}19 \text{ Gt C y}^{-1}$), although this comes at the cost of reduced microherbivory. Estimates of mesozooplankton biomass production (4.2 Gt C y^{-1}) and fecal pellet production (6.2 Gt C y^{-1}) from the present analysis are upper limits for zooplankton contributions to carbon transfer to higher trophic levels and to export of sinking POC from the upper ocean because they do not consider various processes that might lower their magnitudes (Dilling & Alldredge 2000, Anderson et al. 2013).

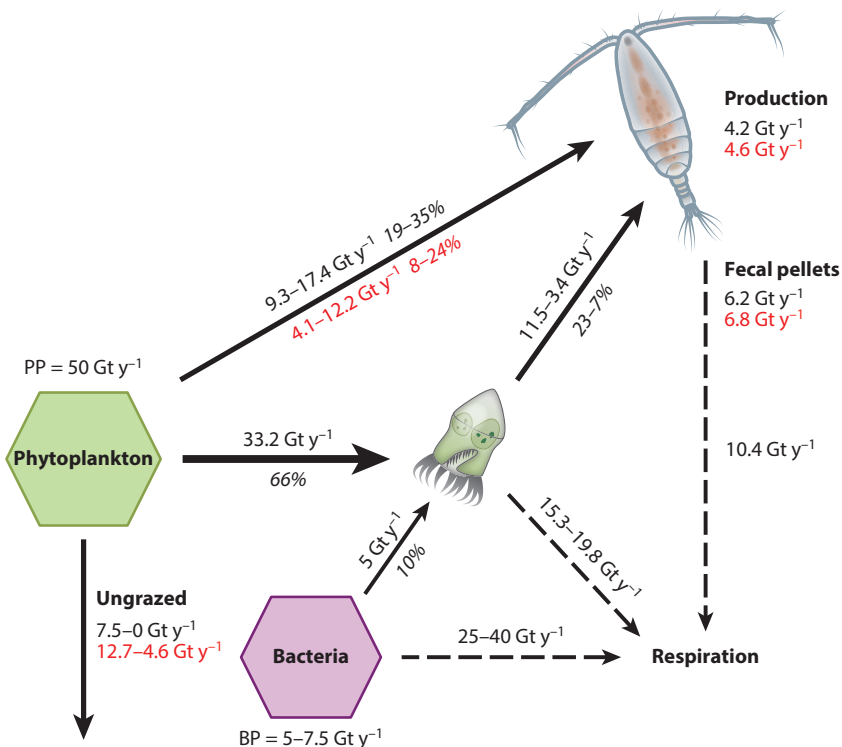


Figure 3

Zooplankton-mediated carbon fluxes in marine epipelagic food webs. The global carbon flux balances for epipelagic food webs shown here emphasize alternative scenarios of trophic structure and carbon flow through micro- and mesozooplankton, represented by a ciliate (*center*) and copepod (*top right*), respectively. All estimates are scaled to a global primary production (PP) of 50 Gt C y⁻¹; numbers in italics are percentages of this total. The major constraints are set by microzooplankton herbivory (based on data in Schmoker et al. 2013) and global estimates of mesozooplankton respiration (Hernández-León & Ikeda 2005a). Alternative scenarios for microzooplankton trophic structure are given by ranges in flux estimates to mesozooplankton and ungrazed phytoplankton: The first number is the value with one trophic level (e.g., ciliates) between phytoplankton and mesozooplankton, and the second is the value with two intermediate levels of consumers (e.g., flagellates and ciliates). Alternative scenarios for mesozooplankton trophic structure are shown in different font colors: Black denotes values when no cycling occurs within the mesozooplankton, and red denotes values when mesozooplankton internally consume 50% of their biomass production and 50% of their fecal pellet production. Additional abbreviation: BP, bacteria production.

Whether mesozooplankton achieve such high grazing impacts on average or have other means of satisfying their energetic requirements are important issues that emerge from this analysis. Feeding on phytoplankton aggregates is assumed to be already incorporated into the grazing estimates based on the measured uptake or disappearance of chlorophyll *a*, so that offers no new nutritional source. However, mesozooplankton are well known to disrupt, consume, and derive significant nutrition from fecal pellets (Dilling et al. 1998, Dilling & Alldredge 2000). If they consume half of their fecal pellet production with a relatively high AE (Dilling et al. 1998) before leaving the euphotic zone, that level of coprophagy could contribute 3.1 Gt C y⁻¹ to ingestion that would not have to come directly from phytoplankton. The remaining nutritional resource is carnivory within the mesozooplankton size fraction. If half of mesozooplankton biomass production is utilized by

carnivorous zooplankton, an additional 2.1 Gt C y⁻¹ of ingestion would not have to come directly from herbivory. In **Figure 3**, we use the sum of these alternative dietary sources (5.2 Gt C y⁻¹, i.e., rates shown in black minus those in red in **Figure 3**), which is almost as large as the previous estimate for mesozooplankton herbivory, to set a lower limit for phytoplankton consumption that is consistent with metabolic constraints. For mesozooplankton grazing on phytoplankton, the range of 4.1–17.4 Gt C y⁻¹ (8–35% of PP) thus includes some consideration of carbon cycling uncertainties for mesozooplankton as well as microzooplankton trophic structure. The lower value establishes the conditions under which mesozooplankton herbivory of the order suggested by Calbet (2001), 12% of PP, would be consistent with their global respiration estimates—a short, efficient trophic structure (one microzooplankton step) and significant carbon inputs from coprophagy and carnivory.

The remaining fluxes in the carbon budget highlight zooplankton roles in the cycling of fixed carbon back to inorganic constituents (i.e., upper-water-column remineralization). Micro- and mesozooplankton respire 31–40% (15.3–19.8 Gt C y⁻¹) and 21% (10.4 Gt C y⁻¹) of PP, respectively, with bacteria likely accounting for an additional 50–90% (Anderson & Ducklow 2001, Rivkin & Legendre 2001). This part of the budget is poorly constrained and can easily exceed 100% because the uptake of ¹⁴C-labeled bicarbonate into particulates over 24-h incubations, the standard for PP measurements in the ocean, often represents only half to a third of total gross PP (Dickson et al. 2001). Similarly, losses of phytoplankton and bacteria to viral lysis are unmeasured by standard dilution experiments (Baudoux et al. 2008, Pasulka et al. 2015), which provide the basis for the proportion of net PP consumed by microzooplankton in this analysis. Thus, they are presumed to be included in microbial cycling processes that make up the difference between gross and net production rates (Landry 2009). Lastly, details of organic fluxes that support bacterial production by various mechanisms (such as sloppy feeding, organic exudation, fecal pellet leaching, viral lysis, and DOC production by phytoplankton) are left unresolved in this analysis.

6.2. Dynamics of Food-Web Coupling

Few studies exist on a regional scale of contemporaneous measurements of micro- and mesozooplankton grazing integrated for the depth range of the euphotic zone, which are necessary for resolving full community grazing impacts relative to integrated phytoplankton production (Landry et al. 2011b). The available studies from tropical and subtropical regions (the Arabian Sea, equatorial Pacific, and Costa Rica Dome) show what might be expected for generally stable, warm, and stratified conditions: a relatively close agreement between phytoplankton production and the combined grazing losses to micro- and mesozooplankton, as well as the direct consumption of virtually all production of the smallest phytoplankton (*Prochlorococcus*, *Synechococcus*, and picoeukaryotes) by microzooplankton (Landry 2009; Landry et al. 2011a, 2016). Similarly efficient coupling of production, grazing, and presumably nutrient recycling occurs during the stratified nutrient-deficient periods of more dynamic seasonal environments, such as the North Atlantic (Lenz et al. 1993). This implies that zooplankton typically regulate phytoplankton carbon biomass over a large portion of the ocean by exerting predation pressures that roughly balance phytoplankton production (Banse 1994, Landry et al. 1997), leaving little unconsumed in the euphotic zone. However, physical or chemical disruptions of that production-grazing coupling can lead to massive blooms and high potential export of ungrazed phytoplankton (Weeks et al. 1993, Legendre & Rivkin 2002, Irigoien et al. 2005, Behrenfeld 2010, Martin et al. 2011, Behrenfeld & Boss 2014). Regional or temporal variability in food-web dynamics that disrupts the production-grazing coupling can consequently

lead to high variability in the zooplankton contribution to passively sinking particulate organic matter, as judged by the biomass of recognizable fecal pellets relative to total export.

In the food-web flux analysis above (**Figure 3**), the amount of PP that escapes zooplankton consumption in the upper ocean ranges from 0% to 25% of PP, depending on trophic structure assumptions. For a minimal one level of microzooplankton consumers and assuming that half of zooplankton production is consumed by carnivorous zooplankton, 9.8 Gt C y⁻¹ (20% of PP) would escape consumption, approximately 50% higher than the estimated mesozooplankton production of fecal pellets (6.2 Gt C y⁻¹). However, this depends strongly on the mean trophic pathway of microzooplankton production to mesozooplankton. Nonetheless, over varying ocean systems and conditions, the contribution of recognizable fecal pellets to total POC export ranges from <1% to ~100%, with most contributions estimated at <40% of POC flux (Turner 2015). Reasonable assumptions about food-web structure and fluxes can clearly arrive at estimates in this range.

Phagotrophy:
feeding by ingesting
organisms or organic
particles

6.3. Trophic Position and Mixotrophy

The importance of understanding the trophic structure of pelagic food webs is highlighted in **Figure 3** by the substantial uncertainties in carbon flows to mesozooplankton resulting from the alternative configurations of the microbial food web (one step or two). This can be further complicated by adding consideration of protistan mixotrophy. There is little doubt that mixotrophy is an important nutritional strategy for plastidic (chlorophyll-containing) cells, particularly in open-ocean oligotrophic systems, where the ability to acquire nutrients by phagotrophy avoids direct competition with bacteria for uptake of dissolved nutrients (Thingstad et al. 1996). Field studies have suggested that many or most of the cells considered to be phytoflagellates in open-ocean systems might be functionally mixotrophic (Unrein et al. 2007, Zubkov & Tarran 2008, Stukel et al. 2011, Hartmann et al. 2012, Sanders & Gast 2012). As argued persuasively by Mitra et al. (2014), widespread mixotrophy should enhance nutrient recycling efficiency via direct consumption of bacterial production by primary producers, and given the availability of photosynthetic carbon fixation to satisfy metabolic demands and a higher efficiency of converting carbon ingested to cell growth (GGE), it should also improve the transfer efficiency of production to higher consumers. With these points in mind, we consider some implications of mixotrophy for the fluxes depicted in **Figure 3**.

First, any direct consumption of mixotrophs by mesozooplankton must already be included in the estimates of mesozooplankton herbivory from Calbet (2001) by virtue of the fact that these grazing impacts were derived from measured rates of consumption (by either cell disappearance or gut fluorescence) of pigmented cells. Direct consumption of mixotrophs, therefore, does not resolve the herbivory shortfall for satisfying metabolic requirements, but could actually increase that shortfall to the extent that it diminishes fluxes that would otherwise be assumed to come from predation on microzooplankton. Second, direct consumption of bacteria by mixotrophs would mean, in the extreme, that bacterial production is incorporated in the production attributed to phytoplankton rather than providing a separate source of nutrition to microzooplankton. This interpretation arises because the estimates of phytoplankton production consumed by microzooplankton from dilution experiments are based on the measured biomass growth rate of pigmented cells (which includes mixotrophs), rather than ¹⁴C uptake (which would potentially exclude the portion of phytoplankton growth derived from phagotrophy). Thus, mixotrophy might raise the PP basis of **Figure 3** from 50 to 55 Gt C y⁻¹ if bacterial production was converted to phytoplankton with 100% efficiency, but the total relative consumption by microzooplankton (66.3% of 55 Gt C y⁻¹) would remain the same. Although there may be a GGE boost for intermediate levels of mixotrophic grazers that are not consumed directly

by mesozooplankton (and therefore not counted as herbivory), the net impact on food-web carbon fluxes is far from clear. Future studies focused on the details of trophic interactions and energy flows in the microbial portion of pelagic food webs are needed to resolve this interesting question.

Independent of the role of mixotrophy, the mean trophic position of mesozooplankton relative to phytoplankton remains a key unknown for assessing regional and temporal variability in the transfer of zooplankton production to higher trophic levels. Most fisheries models assume, for example, that suspension-feeding mesozooplankton are the primary consumers of phytoplankton (trophic position = 2) (Pauly & Christensen 1995, Pauly et al. 2002), and standard isotopic approaches for estimating trophic positions fail to resolve the trophic steps associated with protistan consumers (Hannides et al. 2009a,b; Gutiérrez-Rodríguez et al. 2014). New perspectives and approaches are thus also needed for the higher levels of pelagic food webs to account for the trophic complexities of zooplankton.

7. THE ROLE OF ZOOPLANKTON IN THE BIOLOGICAL PUMP AND CARBON EXPORT

7.1. Particle Production and Carbon Export

Zooplankton can be substantial contributors to POC export through their production of sinking fecal pellets, mucous feeding webs, molts (crustacean exoskeletons), and carcasses (**Figure 1**). The contribution of fecal pellet carbon to total sinking POC flux varies widely among regions, seasons, and depths (see compilations in Turner 2002, 2015; Wilson et al. 2013; and Steinberg 2017) and is dependent on many factors, including the size distribution, species composition, and abundance or biomass of both the zooplankton community and their food (Dagg et al. 2014). These regional differences are illustrated in **Figure 4** and discussed further below. Zooplankton size and species composition in particular affect pellet sinking rates, which range from tens to hundreds of meters per day for copepod and euphausiid pellets (e.g., Yoon et al. 2001) to more than 1,000 m d⁻¹ for salps (Phillips et al. 2009). Mini-pellets (Gowing & Silver 1985) produced by microzooplankton can contribute to POC export as well (e.g., Buck et al. 2005, Lampitt et al. 2009). Many measurements of fecal pellet carbon fall below approximately 40% of total POC flux (Turner 2015), but these estimates are likely conservative, as pellets can break apart in traps and become indistinguishable from aggregates of other origin (Wilson et al. 2008), although the use of polyacrylamide gels helps retain pellet structure (e.g., Ebersbach & Trull 2008).

Under what conditions, then, are fecal pellets predicted to be a major component of the sinking POC flux? The size structure and biomass of the grazer community are clearly key. In a comparison between the subarctic and subtropical North Pacific, large fecal pellets produced by a large *Neocalanus* sp. copepod and a high copepod biomass led to higher carbon export efficiency in the subarctic Pacific (Wilson et al. 2008) (**Figure 4g**). Using a model of copepod fecal pellet carbon flux in the Gulf of Maine, Stamieszkin et al. (2015) showed that copepod size, rather than abundance, is the master trait determining the fraction of copepod fecal pellet carbon that reaches depth. POC flux measured over the continental shelf of the western Antarctic Peninsula is dominated by fecal pellets, mostly from large Antarctic krill (**Figure 4e**), which constitute 67% of the total POC flux in summer compared with 34% in winter, when krill abundance is low (Gleiber et al. 2012). Dagg et al. (2014) also found that episodic events of high fecal pellet flux off the California coast required conditions of both high concentrations of large phytoplankton and diel migrating euphausiids. Likewise, fecal pellets contributed a higher proportion of total POC export (close to 100%) in a coastal upwelling system off California during the productive spring period than they did in the

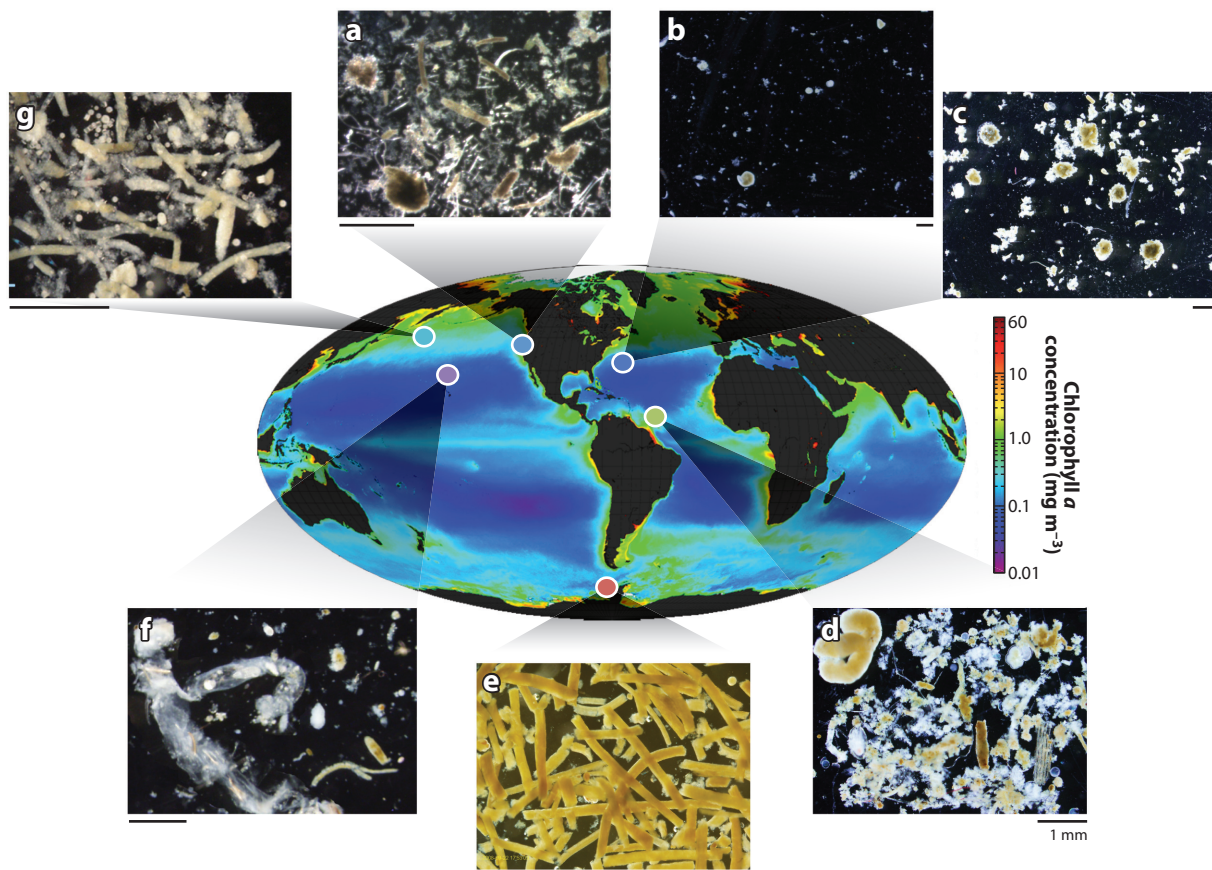


Figure 4

Zooplankton fecal pellets and other detritus in sediment traps deployed at the base of the epipelagic zone (100–170 m) around the world, overlaid on a SeaWiFS (Sea-Viewing Wide Field-of-View Sensor) ocean color chlorophyll *a* map (from <http://earthobservatory.nasa.gov/IOTD/view.php?id=4097>). (a) An upwelling region off the California coast, showing a mix of copepod fecal pellets, diatom debris, and a salp pellet (lower left). (b,c) The Bermuda Atlantic Time-series Study (BATS) station in the North Atlantic subtropical gyre, showing a typical trap sample with small crustacean pellets (panel b) and a large export of salp pellets from a salp bloom (panel c). (d) The Amazon River plume in the tropical North Atlantic, showing a mix of crustacean fecal pellets and pellets of unknown origin (top left). (e) The western Antarctic Peninsula, showing a trap sample over the continental shelf that is composed almost exclusively of Antarctic krill (*Euphausia superba*) fecal pellets. (f) Hawaii Ocean Time-series (HOT) station ALOHA in the North Pacific subtropical gyre, showing copepod and euphausiid pellets and a large heteropod pellet (far left). (g) The subarctic North Pacific, showing abundant copepod fecal pellets from the large copepods *Neocalanus* spp. The scale bars below each image are 1 mm. Photos are from M. Stukel (panel a), D.K. Steinberg (panels b–d), M. Gleiber (panel e), and Wilson et al. (2008) (panels f and g).

fall (Stukel et al. 2013) (Figure 4a). Interestingly, Wilson et al. (2013) found that fecal pellets constituted a greater proportion of abyssal POC flux in the northeast Pacific during periods of lower total POC fluxes, when fecal pellets may be a relatively more important food source for deep-sea communities. High export can also occur during blooms of gelatinous zooplankton (such as salps) that produce large, fast-sinking pellets (compare Figure 4b and Figure 4c). In years with large salp blooms off Bermuda, the maximum annually averaged salp-mediated carbon export (most of which is fecal pellets) equated to 60% of trap POC flux at 200 m (Stone & Steinberg 2016).

Repackaging:

the consumption by zooplankton of suspended or sinking particles (e.g., fecal pellets) and re-egestion as “new” fecal pellets

Swimmers:

zooplankton that swim into sediment traps and die there, as opposed to entering traps as sinking particles (i.e., carcasses)

Certainly many other factors control carbon export by fecal pellets. Fecal pellets are altered as they sink, and their contribution to export changes with depth because of bacterial degradation (Smith et al. 1992, Thor et al. 2003, Tang 2005) and fragmentation (Poulsen & Kiørboe 2005) or ingestion and repackaging by mesopelagic consumers (Steinberg et al. 2008a, Wilson et al. 2008) (see also Section 7.3). Indeed, most fecal pellets produced in the upper mixed layer are degraded by zooplankton such as ciliates, heterotrophic flagellates, and copepods, resulting in retention and recycling of fecal carbon in surface waters (Poulsen & Iversen 2008, Svensen et al. 2012). The composition and sinking rate of fecal pellets are affected by diet and the kinetics of food processing, as described in Section 3. Physical features also affect fecal pellet export directly, as when density discontinuity layers can cause retention of pellets in surface waters (Alldredge et al. 1987), or indirectly, as when fronts or mesoscale eddies concentrate zooplankton or change their assemblage structure and consequently fecal pellet export (Goldthwait & Steinberg 2008, Shatova et al. 2012).

Several zooplankton taxa, particularly appendicularians (larvaceans) but also pteropods and pelagic foraminifera, produce mucous feeding webs that contribute to POC export. Larvaceans use their mucous houses to filter and concentrate food particles, and when the house filters become clogged, the house is discarded, including attached noningested particles plus the larvacean's fecal pellets (Alldredge et al. 2005). Larvaceans may secrete and discard up to 26 houses per day (Sato et al. 2001), and these houses then sink at rates of 10–800 m d⁻¹ depending on their size, age, and other factors (Robison et al. 2005, Lombard & Kiørboe 2010). Because of the fine mesh of their feeding filter, larvaceans can concentrate and ingest particles as small as 0.2 μm (Flood & Deibel 1998, Lombard et al. 2011), and thus their discarded houses and fecal pellets are vehicles for small, slow- or nonsinking cells to be rapidly exported to depth. Discarded houses of two abundant, ubiquitous larvacean species can contribute 12–83% (typically 28–39%) of total POC flux from surface waters in a range of eutrophic coastal and oligotrophic oceanic environments (Alldredge et al. 2005).

Dead zooplankton, including carcasses of crustacean and gelatinous zooplankton, are increasingly recognized as important agents of carbon export. It is challenging to measure the magnitude of this flux, however, because formalin-poisoned sediment traps are commonly used to measure POC export, making it difficult to distinguish carcasses from swimmers that entered traps live and then died there (Buesseler et al. 2007, Frangoulis et al. 2011; but see Sampei et al. 2009). Furthermore, large gelatinous zooplankton carcasses are not sampled by most sediment-trap designs. Copepod carcasses are abundant in the plankton (Tang et al. 2006, Elliott & Tang 2011), and swimmer exclusion devices in sediment traps have shown that the POC and particulate organic nitrogen fluxes by these carcasses exceed those by fecal pellets in the western Mediterranean Sea (Frangoulis et al. 2011). Using the postmortem position of copepod antennules and swimming legs to separate swimmers from true carcasses in sediment traps, Sampei et al. (2012) calculated that the contribution of copepod carcasses to total POC flux in the Beaufort Sea was highest in winter to early spring (16–91%) compared with other seasons (1–30%). Although POC export associated with some larger microzooplankton, such as tintinnids, can be significant (Romero-Ibarra & Silverberg 2011), these probably enter traps on marine snow as living members of the decomposer community.

Jelly falls—the mass sinking of carcasses of bloom-forming gelatinous zooplankton—have been reported from around the world and episodically may lead to substantial, rapid export of POC to deep ocean depths (reviewed in Lebrato et al. 2012) (**Figure 1**). The most commonly recorded jelly falls are medusae (Billett et al. 2006, Yamamoto et al. 2008, Sweetman & Chapman 2011), large colonial pyrosomes (Lebrato & Jones 2009, Lebrato et al. 2013b), and salps (Henschke et al. 2013, Smith et al. 2014). Because of the high sinking rates of jellies, the export efficiency of jelly carbon is calculated to be high, especially at higher latitudes, where colder seawater temperatures reduce rates of microbial decomposition (Lebrato et al. 2013a). The portion of jelly carcasses that

are intercepted in the water column by pelagic consumers is unknown, but once on the benthos, they can be rapidly consumed by deep-sea scavengers (Lebrato & Jones 2009, Sweetman et al. 2014). Although gelatinous zooplankton are considered low in individual carbon and nitrogen content compared with crustaceans of comparable size (Lucas et al. 2011), large species have a relatively high carbon content (Henschke et al. 2013), and the potential for substantial export is high for all bloom-forming species.

Active transport: the transfer of carbon and nutrients from the surface ocean to depth via zooplankton vertical migrations

7.2. Vertical Migration and Active Transport

Diel vertical migration (DVM)—the mass vertical movement of zooplankton (and fish) across the world's oceans between surface waters, where they feed at night, and the mesopelagic zone, where they reside during the day—is another major zooplankton-mediated carbon export pathway (**Figure 1**). When considered as a component of the biological pump, DVM is referred to as active transport, to distinguish it from passive sinking of particles as measured by sediment traps (or by ^{234}Th : ^{238}U disequilibrium). Some of the POC ingested in surface waters each night by diel migrators is transferred (i.e., respired as CO_2 , excreted as DOC, or egested as POC in fecal pellets) at their daytime residence depths below the euphotic zone, and this flux can be significant compared with sinking POC flux (e.g., Longhurst et al. 1990, Steinberg et al. 2000). Although difficult to quantify and thus not always included, the mortality of diel migrators at depth is an additional flux to the deep ocean (Zhang & Dam 1997, Al-Mutairi & Landry 2001). Active transport of DOC and POC by DVM has also been suggested as a source of organic carbon to help satisfy the metabolic demands of resident mesopelagic zooplankton and microbial communities at depth (Steinberg et al. 2008a, Alonso-González et al. 2013; see also Section 7.3). Furthermore, the C:N:P stoichiometry of dissolved inorganic and organic matter produced at depth by migrators can be non-Redfield, potentially contributing to deep nutrient-ratio anomalies (Steinberg et al. 2002) and preferential export of some elements—as is the case for phosphorus in the North Pacific subtropical gyre (Hannides et al. 2009a,b).

The magnitude of active transport by diel migrating zooplankton and the relative importance of active as opposed to passive transport vary regionally and seasonally, depending on migrator biomass and taxonomic composition (see compilations in Takahashi et al. 2009, Putzeys et al. 2011, and Isla et al. 2015). Active transport of respiratory carbon generally increases with higher migrator biomass (**Figure 5a**), and a higher respiratory flux results in the increasing importance of active transport compared with passive sinking of POC (**Figure 5b**). Care must be taken in comparing ecosystems, as some studies report only respiratory flux, whereas others include additional active fluxes such as DOC excretion, fecal pellet production, mortality at depth, or various combinations thereof. Active transport also becomes relatively more important in carbon export with increasing depth, as sinking particle flux decreases rapidly with increasing depth. Keeping these considerations in mind, published studies have generally indicated higher migrant biomass and active respiratory flux in more productive upwelling and coastal/mesotrophic ecosystems or seasons compared with less productive oligotrophic systems or seasons. This trend is also apparent in biogeochemical models of active transport by DVM (Bianchi et al. 2013). For example, in the mesotrophic subarctic Pacific, the active transport of CO_2 and DOC by migrator respiration and excretion was $16\text{--}46 \text{ mg C m}^{-2} \text{ d}^{-1}$ (equivalent to 26–200% of sinking POC) measured by sediment traps at 150 m, compared with $2\text{--}8 \text{ mg C m}^{-2} \text{ d}^{-1}$ (equivalent to 11–44% of sinking POC) in the oligotrophic North Pacific subtropical gyre (Steinberg et al. 2008b). However, the importance of active transport by DVM compared with passive sinking of particles is not necessarily higher in more productive ecosystems or conditions, as low sinking POC fluxes in oligotrophic regions would increase the relative importance of active transport. Additionally, in regions with

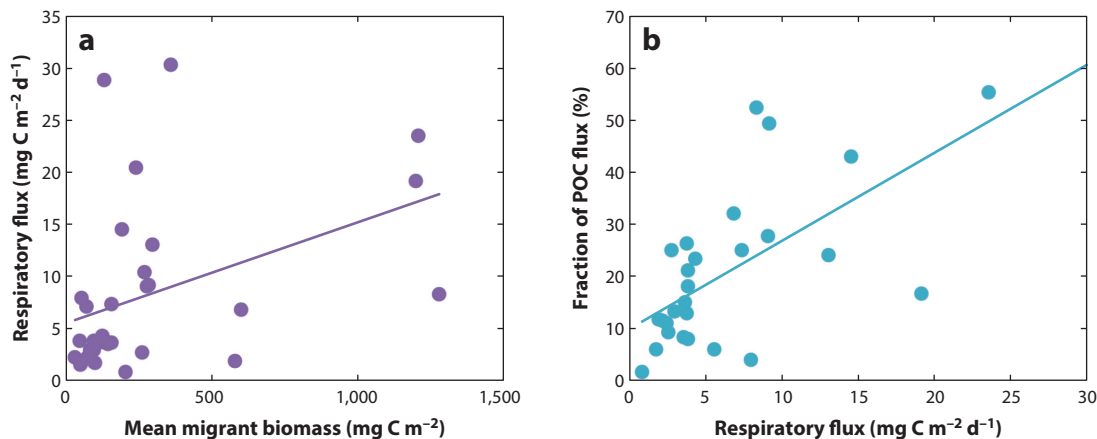


Figure 5

Respiratory flux by diel vertical migration. Data are compiled from studies in a variety of locations in the North Atlantic and Pacific and during different times of the year, showing (a) mean migrant biomass (night minus day biomass in the epipelagic zone) versus mean respiratory (CO_2) flux by diel vertical migration and (b) mean respiratory flux versus the equivalent fraction of particulate organic carbon (POC) export from the epipelagic zone measured by sediment traps at 100–200 m. The sources for the data are given in the **Supplemental Appendix** (follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>).

Supplemental Material

pronounced OMZs, active transport of respiratory CO_2 by DVM may be reduced, as low-oxygen conditions depress the respiration and excretion rates of some taxa (Kiko et al. 2015).

Another form of active transport of carbon is by ontogenetic (seasonal) vertical migration. Best known for large subarctic copepods (e.g., *Calanus* spp. in the North Atlantic and *Neocalanus* spp. in the North Pacific), the metabolism and mortality of overwintering adults at depth can annually account for significant carbon export compared with passive sinking of POC. Near the end of the spring bloom, adult copepods migrate to mesopelagic depths, where they spawn and eventually die or are eaten by predators (or undergo diapause, a resting stage, if they have a life cycle of longer than one year). Early estimates of active transport by seasonal migration in the subarctic North Atlantic were low (Longhurst & Williams 1992), but Jónasdóttir et al. (2015) showed that transport and metabolism of carbon-rich lipids by *Calanus finmarchicus* migrating annually to depths of 600–1,400 m result in a carbon export equivalent to the deep sinking POC flux. Importantly, this lipid pump is a direct transport of carbon below the permanent thermocline, with little attenuation, that nearly doubles previous estimates of deep-ocean carbon sequestration in the North Atlantic (Jónasdóttir et al. 2015). Similarly, at higher latitudes in the Arctic Ocean, seasonally migrating *Calanus* spp. (mostly large herbivorous *C. hyperboreus* and *C. glacialis*) actively transport $3.1 \text{ g C m}^{-2} \text{ y}^{-1}$ below 100 m, representing $\sim 85\text{--}132\%$ of the annual 100-m POC passive flux, owing to the exceptionally large lipid reserves in arctic zooplankton from spring grazing, which are respired at depth during a long overwinter period (Darnis & Fortier 2012). In the subarctic North Pacific, active transport by seasonal migration of *Neocalanus* spp. copepods (*N. flemingeri*, *N. cristatus*, and *N. plumchrus*) is comparably high, ranging from 2.0 to $4.3 \text{ g C m}^{-2} \text{ y}^{-1}$ below 150 m (Kobari et al. 2003, 2008). Similarly, in the subantarctic Southern Ocean, active transport by *N. tonsus* is $1.7\text{--}9.3 \text{ g C m}^{-2} \text{ y}^{-1}$ (Bradford-Grieve et al. 2001).

7.3. Mesopelagic-Zone Processes

Mesopelagic zooplankton transform POC in sinking and suspended particles by consuming and remineralizing them to CO_2 , repackaging the particles into fecal pellets with different sinking

speeds and organic content (Wilson et al. 2008), or fragmenting sinking POC into smaller and slower-sinking particles via feeding or swimming activities (e.g., Goldthwait et al. 2004, De La Rocha & Passow 2007) (**Figure 1**). These processes, along with remineralization by bacteria, cause a rapid attenuation of sinking POC with depth through the mesopelagic zone (Steinberg et al. 2008a, Robinson et al. 2010). However, by feeding in surface waters and defecating at their mesopelagic residence depths, diel vertical migrants create a vertical shunt that enhances POC flux at depth but is missed by most sediment traps (Buesseler & Boyd 2009). Despite considerable evidence from both gut contents (Lampitt et al. 1993, Steinberg 1995, Schnetzer & Steinberg 2002) and changes in particle abundances and size spectra with depth (Bishop & Wood 2009) that mesopelagic zooplankton consume sinking particles, measurements of feeding rates on detritus are rare (Dilling et al. 1998). Suspended particles can be repackaged to form new sinking particles at depth, for example, by the mucous feeding webs of larvaceans (see Section 7.1), and as evidenced by changing fecal pellet types with increasing depth (Wilson et al. 2008). Conversely, zooplankton fragmentation of large detrital particles into smaller ones with larger surface areas that promote growth of resident bacteria and protistan consumers has been suggested to increase the nutritional content of otherwise poor substrates. This microbial gardening makes it more nutritionally and energetically beneficial for zooplankton to fragment rather than ingest large particles directly (Mayor et al. 2014).

The surface-ocean carbon supply ultimately fuels the metabolic requirements of the mesopelagic community; however, regional measurements of POC export plus downward advection of DOC to the mesopelagic zone are often too low to meet the carbon demand by mesopelagic zooplankton and bacteria (Steinberg et al. 2008a, Burd et al. 2010). Reconciling this apparent mismatch has been a focus of recent studies. This carbon demand is partially met by DVM of zooplankton feeding at the surface and by carnivory at depth, both of which are independent of the consumption of sinking POC (Steinberg et al. 2008a). Other zooplankton-mediated processes, such as fragmentation of large sinking particles or release of DOC from excretion or sloppy feeding, can help fuel mesopelagic microbial metabolism and supply carbon back to the food web (Anderson & Tang 2010, Giering et al. 2014). In addition, chemoautotrophic CO₂ fixation supports abundant Crenarchaeota in the deep ocean and provides a source of autochthonous “new” organic carbon to support mesopelagic food webs (Reinthal et al. 2010). An additional consideration is uncertainty in measurements and conversion factors, such as mesopelagic zooplankton diets and AE, bacteria growth efficiency, or pressure effects on metabolic rates (Steinberg et al. 2008a, Burd et al. 2010). Giering et al. (2014) balanced a carbon budget for the mesopelagic zone at a North Atlantic site in part by using the mixed-layer depth as the dynamic upper boundary of the mesopelagic zone, rather than a set euphotic-zone depth. In sum, carbon transformations by zooplankton and interactions between microbes and metazoans in the mesopelagic zone have yet to be fully characterized and are needed to constrain and balance deep-ocean carbon budgets.

8. LONG-TERM AND FUTURE CHANGES IN ZOOPLANKTON CARBON CYCLING

Rising ocean temperatures, decreasing oxygen, ocean acidification (OA), eutrophication, overfishing, and species introductions are changing plankton communities, and synergistic effects of these factors could lead to widespread changes in zooplankton carbon cycling in the coming decades. Temperature affects nearly all aspects of carbon flow through zooplankton either directly (rates of feeding, metabolism, growth, and reproduction; e.g., Kjellerup et al. 2012) or indirectly (e.g., changes in surface-water stratification and vertical mixing affecting prey field). Thus, a warming

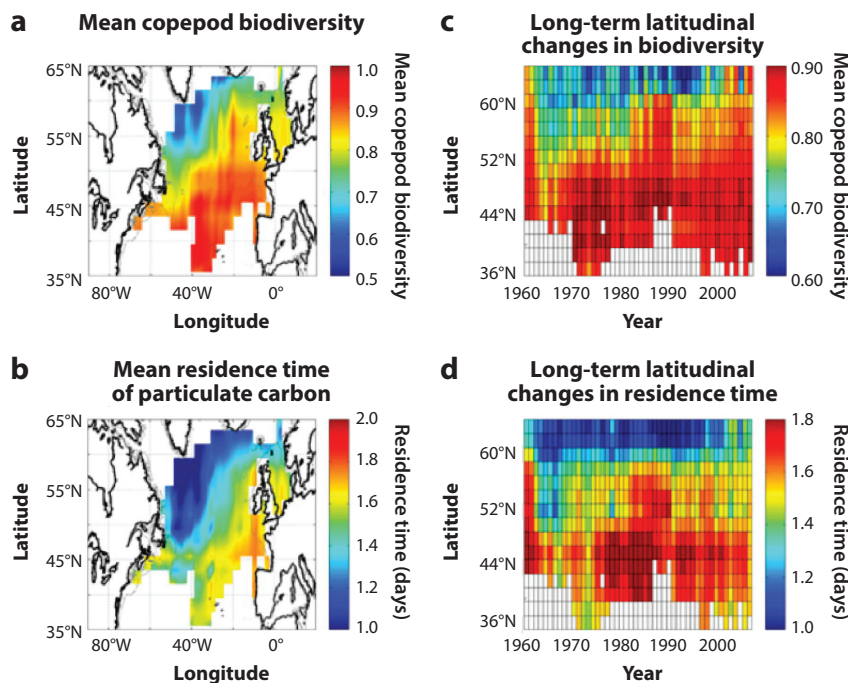


Figure 6

Long-term latitudinal changes in copepod biodiversity and mean residence time above 50 m of sinking copepod fecal pellets in the North Atlantic. (a,b) Mean spatial distributions (for time series from 1960 to 2007) of copepod biodiversity (panel a) and mean residence time of particulate organic carbon in sinking copepod fecal pellets (panel b) above 50 m. (c,d) Long-term latitudinal changes in copepod biodiversity (panel c) and residence time of sinking copepod fecal pellets (panel d) above 50 m, showing an increase in recent decades for both in the north. Copepod biodiversity was measured by a first-order jackknife performed on the Gini coefficient; higher values indicate greater diversity. The residence time of the fecal pellets was modeled from size-derived relationships with copepod body size. Copepod body size, which is negatively correlated with diversity, has been decreasing over time in northern latitudes coincident with warming. Adapted from Beaugrand et al. (2010).

ocean has a multitude of potential effects, including alteration of the relative rates of production and grazing resulting from different temperature dependencies of autotrophic and heterotrophic rate processes, as suggested by the metabolic theory of ecology (e.g., Brown et al. 2004, Rose & Caron 2007, Chen et al. 2012). Long-term changes in epipelagic zooplankton abundance, distribution, and community structure in many regions are attributed to climate warming, with associated changes in carbon cycling. In the North Sea, increasing sea-surface temperature has led to a long-term decrease in the subarctic herbivorous copepod *C. finmarchicus* accompanied by a long-term increase in large phytoplankton; the suggested mechanism for the latter is reduced grazing pressure on diatoms, which would be predicted to increase export of diatom aggregates and overall carbon export (Beaugrand 2009). However, a long-term increase in calanoid copepod biodiversity and a decrease in body size in the same region lead to a modeled increase in the mean residence time of sinking copepod fecal pellets (owing to their smaller size) above 50 m, potentially reducing carbon export (Beaugrand et al. 2010) (**Figure 6**).

In the North Atlantic subtropical gyre, a long-term increase in epipelagic mesozooplankton biomass was positively correlated with sea-surface temperature, water-column stratification, and

PP, resulting in increased annual fecal pellet carbon export and a near doubling of diel vertical migrator biomass and active transport of carbon (Steinberg et al. 2012). A long-term decline in the carbon biomass of pelagic tunicates (mostly salps) in the California Current in the eastern Pacific was also associated with increased water-column-density stratification and was consistent with a long-term decline in the 3,500–4,000-m POC flux until approximately 1999 (Smith et al. 2006, Lavaniegos & Ohman 2007). In more recent years, episodic pulses of high salp biomass and sinking POC as salp fecal pellets have been recorded in the same region (along with salp carcasses, described above; Smith et al. 2014). A sea-surface-temperature warming anomaly from 2005 to 2007 in the Fram Strait entrance to the Arctic Ocean shifted the community structures of both phytoplankton and zooplankton and decreased export flux. Lower fecal pellet carbon flux and export of smaller fecal pellets during the warm period coincided with lower biogenic silica fluxes, suggesting a change in feeding conditions from larger zooplankton feeding on diatoms to smaller zooplankton feeding on smaller-sized phytoplankton (coccolithophores) (Lalande et al. 2013).

Ocean deoxygenation, including spreading coastal hypoxia and dead zones (Diaz & Rosenberg 2008, Levin & Breitburg 2015) and the global expansion of OMZs (Stramma et al. 2008, 2010; Gilly et al. 2013), will likely have marked effects on zooplankton carbon cycling. The oxygen gradients associated with OMZs structure zooplankton communities (Wishner et al. 2013), and hypoxia can suppress zooplankton respiration rates (Maas et al. 2012, Teuber et al. 2013, Cass & Daley 2014). Respiration by diel vertically migrating zooplankton intensifies oxygen depletion in the upper margins of OMZs, focusing remineralization of organic carbon at these boundaries (Bianchi et al. 2013). Other processes attributed to strong vertical gradients in biological communities across OMZs could enhance carbon export relative to non-OMZ regions. Roullier et al. (2014), for example, found changes in particle size distribution, as well as increased particle abundance, zooplankton abundance, and calculated carbon export in the lower oxycline of the Arabian Sea OMZ, attributed in part to enhanced zooplankton feeding in the deep OMZ. A metabolic index that combines the effects of increased ocean temperature and decreased oxygen predicted global habitat compression of plankton biogeographic ranges (both poleward retreat and vertical contraction) (Deutsch et al. 2015), which may serve to focus or intensify zooplankton-mediated carbon exchange and export in these regions.

Absorption of increased atmospheric CO₂ from human activity into ocean surface waters has led to OA, “the other CO₂ problem” (Doney et al. 2009). Known effects of increased CO₂ and OA on zooplankton carbon cycling include metabolic suppression, as evidenced by decreased respiration rates in Antarctic pteropods (although the effect is modulated by food concentration; Seibel et al. 2012) and in tropical reef coral larvae (Rivest & Hofmann 2014). Most calcifying organisms exhibit reduced calcification in response to OA (although there are exceptions; Riebesell et al. 2000) and sometimes dissolution of their shells and skeletons (Fabry et al. 2008). Ballast provided by calcite and opal significantly increased the sinking speed of fecal pellets produced by copepods fed coccolithophorid and diatom diets, respectively, over the sinking speed of pellets from copepods fed nanoflagellates (Ploug et al. 2008). A future decrease in carbonate ballast in fecal pellets and other particles would slow their sinking rates, resulting in more organic matter being remineralized shallower in the water column (Bishop & Wood 2009), which would reduce carbon sequestration flux (Passow & Carlson 2012). Although research has made great strides in elucidating the effects of OA on marine organisms and ecosystems, the physiological and other effects of OA on zooplankton have been studied in only a handful of taxa, and thus the consequent effects on zooplankton and carbon cycling are largely unknown.

SUMMARY POINTS

1. Carbon flows through marine pelagic ecosystems are complicated by the phylogenetic and functional diversity of planktonic consumers and the complex and multilevel trophic organization of the food webs in which they operate.
2. At the extremes, zooplankton-mediated food-web linkages underlie the highly efficient nutrient recycling that sustains high levels of phytoplankton productivity in the oligotrophic open oceans, as well as the efficient transfer of primary production to higher trophic levels in the ocean's richer regions.
3. Zooplankton impacts on ocean biogeochemical cycles are further complicated by the variable efficiencies of bioenergetic processes (absorption, respiration, excretion, and growth) that transform carbon fluxes through individuals and populations into dissolved and particulate products with different food-web fates.
4. Carbon fluxes through the zooplankton are constrained on the global scale by the grazing impacts of microzooplankton and the respiratory requirements of mesozooplankton, as affected by biomass, size, and temperature.
5. Dissolved organic carbon release by zooplankton via sloppy feeding, excretion, egestion of dissolved digestive products, and fecal pellet leaching supports an active microbial loop.
6. Zooplankton contribute to biological pump export processes through a variety of mechanisms (mucous feeding webs, fecal pellets, molts, carcasses, and vertical migrations). The relative importance of these different export mechanisms and the magnitude of their combined contributions to carbon transfer into the ocean interior are highly dependent on regionally variable plankton community structure.
7. Increasing ocean temperatures, decreasing oxygen, ocean acidification, eutrophication, overfishing, and species introductions are already affecting plankton communities and are predicted to result in widespread changes in zooplankton carbon cycling in the future.

FUTURE ISSUES

1. There is a need to resolve large uncertainties in trophic structure that significantly alter mean outcomes and interpretations of carbon flows through zooplankton in food webs. These uncertainties include, but are not limited to, the mean trophic pathway of microzooplankton production to mesozooplankton, the effects of mixotrophy on food-web efficiency, and the details of linkages between zooplankton and bacteria.
2. Zooplankton roles and food-web controls on remineralization and organic matter degradation in the mesopelagic zone, which are fundamental to defining carbon flux attenuation and export variability, need to be better measured and understood.
3. Significant challenges remain in measuring key carbon flows through zooplankton, such as a standard approach for assessing secondary production, or zooplankton-mediated carbon export not measured by traditional sediment traps (e.g., jelly falls and active transport via vertical migration).

4. How zooplankton affect the stoichiometry between carbon and other key elements (nitrogen and phosphorus) in ocean biogeochemical cycles requires further study.
5. Substantial uncertainties also exist in climate impacts on regional scales, which may follow expected (bottom-up) patterns of ecosystem response to changing temperature, physics, and nutrient delivery or may diverge considerably because of altered biomass and functions of key zooplankton species as a response to stressors.
6. Ecosystem and biogeochemical models, which currently represent the roles of zooplankton simplistically, could better incorporate the diversity in zooplankton taxa, life history, size, trophic ecology, and physiology to improve predictions of future changes in carbon flows through zooplankton.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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