

Insights & Perspectives

Microbial gardening in the ocean's twilight zone: Detritivorous metazoans benefit from fragmenting, rather than ingesting, sinking detritus

Fragmentation of refractory detritus by zooplankton beneath the euphotic zone stimulates the harvestable production of labile and nutritious microbial biomass

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Sinking organic particles transfer ~10 gigatonnes of carbon into the deep ocean each year, keeping the atmospheric CO₂ concentration significantly lower than would otherwise be the case. The exact size of this effect is strongly influenced by biological activity in the ocean's twilight zone (~50–1,000 m beneath the surface). Recent work suggests that the resident zooplankton fragment, rather than ingest, the majority of encountered organic particles, thereby stimulating bacterial proliferation and the deep-ocean microbial food web. Here we speculate that this apparently counterintuitive behaviour is an example of microbial gardening, a strategy that exploits the enzymatic and biosynthetic capabilities of micro-organisms to facilitate the gardener's access to a suite of otherwise unavailable compounds that are essential for metazoan life. We demonstrate the potential gains that zooplankton stand to make from microbial gardening using a simple steady state model, and we suggest avenues for future research.

Keywords:

■ carbon cycling; detritus; mesopelagic; microbial loop; nutrition; polyunsaturated fatty acid; zooplankton



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Abbreviations:

BCP, biological carbon pump; **DHA**, docosahexaenoic acid (22:6(n-3)); **EPA**, eicosapentaenoic acid (20:5(n-3)); **PUFA**, polyunsaturated fatty acid.

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Introduction: Carbon sequestration in the oceans via biological activity

The biological carbon pump (BCP) refers to the suite of processes that store atmospheric CO₂ in the deep ocean via the production of organic matter in the upper ocean and its sinking and subsequent remineralisation at depth. Between 5 and 12 gigatonnes of photosynthetically-fixed carbon leaves the sunlit (euphotic) waters of the upper ocean each year via sinking particles [1]. Typically <10% of this organic matter reaches the deep-seafloor: the vast majority is remineralised to inorganic carbon by the respiration of the organisms that reside in the dimly lit waters of the 'mesopelagic zone', also known as the 'twilight zone'. This begins at the base of the euphotic zone, where photosynthesis is no longer possible, and extends down to ~1,000 m. The depth at which remineralisation occurs plays a major role in determining the size of biological carbon storage in the oceans, and hence the oceanic role in global climate regulation [2]. Understanding the factors influencing the strength of the BCP remains a major goal of biological oceanography.

The twilight zone ecosystem contains a diverse range of prokaryotes and eukaryotes. The microbial web begins with free-living and particle-attached heterotrophic bacteria. These organisms support active communities of heterotrophic flagellates and ciliates, which can be two to four orders of magnitude more abundant on particles than in the surrounding water [3]. The metazoan component of the twilight zone can be broadly categorised as (a) temporary residents that migrate into the cool, deep waters during daylight hours to reduce their metabolic demands and minimise predation pressure from visual predators, and (b) true residents. Feeding in surface waters under the cover of darkness provides temporary residents with sufficient resources to support their daily metabolic demands, eliminating the need for them to feed in the mesopelagic [4]. By contrast, the resident metazoan community, the biomass of which is dominated by copepods ≤ 1 mm [4, 5], tiny crustaceans that swim with rowing-like movements of their fore-legs, must derive their energetic and nutritional requirements at depth through detritivory and/or carnivory.

The collective respiration of organisms resident in the twilight zone should, at steady state, equal the loss of carbon estimated as the reduction in flux as it sinks down through the mesopelagic. Until recently, attempts to demonstrate this balance have failed (e.g. [6]). A balanced budget has, however, now successfully been obtained based on field observations and a modelling study of the twilight zone at the Porcupine Abyssal Plain (PAP) Site (49°N 16° 30'W) in the North Atlantic [4]. A central conclusion of this work is the understanding that whilst the resident microbial and metazoan communities each intercept approximately 50% of the sinking organic matter, the metazoans fragment, rather than ingest, most of the fast-sinking particles that they encounter. The resulting production of smaller, slowly- or non-sinking organic particles stimulates bacterial proliferation and the microbial food web. The low growth efficiencies of bacteria [7] and protozoans [8] necessitates that much of the organic carbon that enters this pathway is ultimately respired. Thus, the carbon budget constructed for the PAP site showed that respiration in the twilight

zone is dominated by the bacteria (79%), and zooplankton account for only a minor fraction (21%) [4].

The question thus arises, why are detritivorous zooplankton such messy feeders, apparently breaking up and releasing sinking organic matter, rather than ingesting it directly as food for processing in the gut? This could reflect a simple necessity; some detrital particles, e.g. the houses of larvaceans (free-swimming tunicates) and the faecal pellets of euphausiids (krill), are far too large to be directly ingested. Here we develop an alternative explanation for why this seemingly wasteful behaviour occurs. The average sinking detrital particle within the twilight zone, which is considerably reworked by zooplankton [9], is difficult to digest, contains little in the way of nutrition and hence is a poor substrate for metazoan growth. We speculate that deliberate fragmentation of large detrital particles, which stimulates its transformation

into smaller particles rich in microbial biomass, is a means by which zooplankton increase the energetic and nutritional content of particulate organic matter for subsequent ingestion (Fig. 1). This is conceptually analogous to the 'microbial gardening' observed in coastal benthic detritivores [10, 11]. An early investigation into microbial gardening [10] demonstrated that apparently detritivorous estuarine amphipods actually consume the detritus-associated microbial community; plant residues pass through the animals undigested. Amphipods encourage, or garden, microbial biomass by fragmenting detritus, causing the numbers of particle-associated bacteria, flagellates, and ciliates to increase rapidly and greatly. Nevertheless, a trade-off exists between ingesting a high-quantity, low-quality detrital diet and a low-quantity, high-quality diet rich in microbes. Here, we articulate the case for microbial gardening as a strategy for maximising fitness

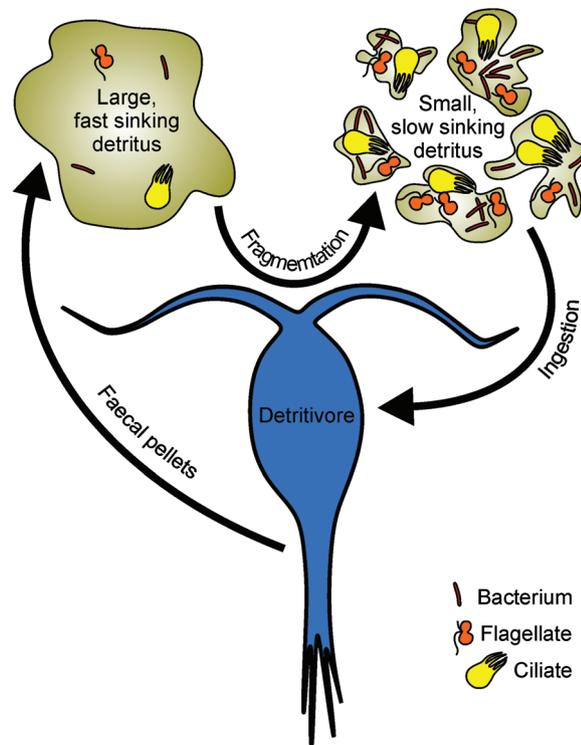


Figure 1. Microbial gardening in the twilight zone. We speculate that detritivorous zooplankton stimulate the production of labile and nutritious microbial biomass by fragmenting, rather than ingesting, large detrital particles. Detritus fragmentation increases the amount of organic matter exposed to bacterial degradation, encouraging their population growth. Increased bacterial biomass fuels the growth of flagellates and ciliates and the concomitant production of essential biochemical compounds. These protists, which are energetically and nutritionally superior to detritus, are sufficiently large to be effectively harvested by the zooplankton. Image not to scale.

in resident mesopelagic zooplankton, and use a simple food web model to demonstrate that it can be an effective growth strategy.

Life in the twilight zone

Twilight zone residents experience hydrostatic pressures of up to 100 bar and temperatures as low as 4 °C. They also face considerable spatial and temporal variability in the distribution of organic substrates, reflecting the heterogeneous distribution of plankton and seasonal productivity patterns, respectively. The attainment of neutral buoyancy helps these animals conserve energy and also reduces the chance of being detected by raptorial predators [12].

Temperature and pressure both affect the functioning of the lipid bilayers that constitute biological membranes [13]. Marine organisms adapt to these physical constraints by changing the fatty acid composition of their cellular membranes [14]. Lipids are also central to how metazoans survive food shortages [15] and attain neutral buoyancy [16]. Recent work has specifically highlighted central roles for the polyunsaturated fatty acids (PUFAs) eicosapentaenoic acid (EPA, 20:5(n-3)) and docosahexaenoic acid (DHA, 22:6(n-3)) in buoyancy control, membrane functionality, and the starvation response of marine copepods [12, 17–19]. Pelagic zooplankton that feed in the euphotic zone principally derive EPA and DHA from ingested diatoms and flagellated microplankton, respectively. They are incapable of synthesising them *de novo* or by the elongation of dietary precursors at ecologically significant rates [20]. Mesopelagic copepods, e.g. *Oithona* spp. and *Oncaea* spp., contain significant quantities of these PUFAs within their body tissues [21], and they likely play similar physiological roles. The origins of EPA and DHA in these animals remain unknown, in part reflecting the complexities associated with discerning the diets of mesopelagic copepods [22].

The majority of sinking organic matter supplied to heterotrophic organisms in the twilight zone is in the form of marine snow, faecal pellets, and other particles of detritus. These particles may have been previously ingested and reworked multiple times by zooplank-

ton that selectively absorb the most labile and nutritious dietary compounds, including essential amino acids and PUFAs [17, 23]. This explains why concentrations of these compounds in suspended particles decline dramatically with depth [24–26], whereas the relative proportions of refractory polysaccharides and the C:N ratio of detritus both increase [27, 28]. The majority of organic matter available to twilight zone residents therefore consists of refractory organic particles that are devoid of compounds thought to be central to life in these waters. An exception to this occurs during the rapid sedimentation of phytoplankton cells, e.g. following diatom blooms, which are known to transport significant quantities of PUFAs down through the mesopelagic and into the abyss [25]. However, the significance of these ephemeral events to twilight zone residents remains unknown. We suggest that deriving the majority of their annual metabolic- and nutritional demands from detritus poses potential problems for metazoans, which typically lack the endogenous enzymatic capacity for the degradation of long chain carbohydrates and biosynthesis of compounds such as EPA and DHA. Thus, zooplankton should in principle exploit any opportunity to enhance the acquisition of these compounds from their diet [29].

Animals that ingest a diet rich in refractory biopolymers, e.g. detritus or cellulose-rich leaves, typically display commensal or symbiotic relationships with intestinal microorganisms, perhaps best exemplified by the ruminant mammals [30]. Some terrestrial and marine invertebrates also display digestive associations with bacteria [31, 32]. These animals have capacious, and often specialised guts that are capable of retaining food for prolonged periods. Pelagic copepods are known to harbour internal microorganisms [33, 34], but the small size of those inhabiting the twilight zone suggests that bacterially-mediated digestion in their guts is unlikely [31, 35].

Microbial gardening

Zooplankton faecal pellets can contribute significantly to carbon export be-

neath the euphotic zone [3]. Flux-feeding [36] copepods fragment, rather than ingest, the majority of encountered faecal material [37–41], and potentially explain why the number of faecal pellets observed beneath the euphotic zone is less than would be expected from the abundance of copepods in the overlying waters. The extension of this mechanism to include the fragmentation of all large detrital particles has recently helped reconceptualise the twilight zone carbon budget [4]. However, the reasons underlying this seemingly wasteful strategy are obscure. Here we suggest that it offers significant energetic and nutritional benefit to the metazoans, despite losses through microbial respiration, which reduces the absolute quantity of available organic matter.

Fragmentation of large, detrital particles reduces their sinking speed [38], locally retaining organic resources that would otherwise sink into the abyss. It also increases their surface area, making them more amenable to bacterial colonisation and hence stimulates microbial pathways [10, 38]. The latter provides two distinct potential benefits to detritivores. Firstly, it exploits the extensive repertoire of bacterial exoenzymes for breaking down the plethora of refractory compounds supplied to the twilight zone, hence obviating the need for these enzymes in the detritivores. Indeed, this process may be a necessity because the degradation of long chain polysaccharides, e.g. cellulose, is enzymatically complex and almost exclusively undertaken by microorganisms [42]. A second, major benefit of stimulating the microbial food web is the ‘trophic upgrading’ of the particulate organic matter: bacteria and heterotrophic protists are both capable of *de novo* synthesis of a range of labile and essential compounds, including EPA and DHA [29, 34, 43, 44]. The net result of fragmenting large, refractory particles of sinking organic matter is the production of slow-sinking particles that are hotspots of microbial activity. The resident flagellates and ciliates represent digestible and nutritious biomass that is of appropriate size for copepods to effectively harvest from the surface of particles.

Our assertion is supported by reports of smaller, slow-settling particles

containing more labile compounds than larger ones [45, 46]. It is also consistent with the idea that twilight zone copepods only feed on a fraction of the total detrital pool [22], potentially selecting particle-attached bacteria [37] and microbes [40]. The drawback to microbial gardening is that it ultimately reduces the absolute quantity of carbon available to the gardeners: attached microbes respire much of their substrate to CO₂ and may be ingested by organisms that do not contribute to fragmentation.

The trade-off between maximising the direct ingestion of low-quality particulate organic detritus versus microbial gardening, i.e. the fragmentation of this material for colonisation by nutritionally-rich microbes that are subsequently ingested, was examined using an adapted version of a simple steady state model [4]. The model follows the utilisation of sinking particles by bacteria and zooplankton and the subsequent cycling of carbon in the detrital food web along three pathways: colonisation and solubilisation of detritus by attached bacteria, consumption of detritus and resident microbial populations by detritivorous zooplankton, and the use of solubilisation products (dissolved organic carbon) by free-living bacteria. Detritus is divided into two types [47]; large, fast-sinking particles (D1) and smaller, slower- or non-sinking particles (D2). The previous implementation of this model [4] assumed that detritivores have grazing access only to the former pool. During grazing, 30% (parameter $\lambda = 0.3$) was released as small, non-sinking material, a further 5% (parameter $r = 0.05$) being excreted as DOC (providing a growth substrate for free-living bacteria). The remainder was used with absorption (digestion) efficiency of 60% (parameter $\beta = 0.6$) and net production efficiency (fraction of absorption used for growth) of 39% (parameter $k = 0.39$) to give a combined growth efficiency of 0.23 (the product of β and k).

Without being able to graze on D2, the potential for microbial gardening was not investigated. We have modified the model by permitting detritivores to graze on the D2 detrital pool and its associated microbial biomass, and by altering key parameters to reflect the contrasting nutritional status of D1 and

D2 for zooplankton (see Supporting Information Figs. S1 and S2 and Table S1). Whereas previously attached bacteria and zooplankton processed D1 equally (parameter $\psi_B = 0.5$) with 100% utilisation of D2 by bacteria, we now use ψ_{B1} and ψ_{B2} of 0.05 and 0.5 for D1 and D2, respectively, reflecting the active growth of microbial populations on D2 and greater zooplankton usage thereof. The efficiencies with which zooplankton utilise compounds and elements is variable [17, 23] but we are unaware of any data relating specifically to twilight zone organisms. Model parameters are therefore chosen to illustrate our hypothesis and are not intended as definitive values.

Detritivorous zooplankton use large particles (D1) with a low absorption efficiency ($\beta_1 = 0.1$) in accordance with the hypothesis that they do not have the capacity to digest the majority of this refractory material. The net production efficiency of absorbed D1 is also assigned a low value ($k_1 = 0.25$) because of increased biosynthesis costs resulting from the nutritional imbalance of compounds in food relative to the requirements of the detritivores [48]. Organic matter in D2, mostly represented by labile and nutritious microbial biomass, is easier to absorb ($\beta_2 = 0.5$) and more closely matches the nutritional requirements of the detritivores. The lower costs of biosynthesis give rise to increased net production efficiency ($k_2 = 0.5$).

The model is clearly a simplification of the full complexity of the twilight zone and represents complex and likely variable terms, e.g. detritus lability, bacterial and zooplankton physiology and ecology, as crude averages in this vertically expansive ecosystem. Nevertheless, it enables us to examine the potential of microbial gardening as a strategy for maximising the growth of detritivorous zooplankton by varying the fraction of D1 fragmented to D2 during grazing (parameter λ). As λ increases, a greater proportion of D1 detritus is fragmented, favouring the ingestion of D2 detritus by zooplankton, the proposed gardening pathway. Ingestion decreases overall (Fig. 2A) because, quantitatively, much of the D2 detrital pool is lost to CO₂ via microbial respiration. Production is lowest when detritivores ingest, rather than frag-

ment, D1 ($\lambda = 0$; Fig. 2B), even though ingestion is greatest. This reflects the low efficiencies with which they can absorb and subsequently utilise this nutritionally inferior material for the production of biomass. Fragmentation of D1 ($\lambda > 0$) increases detritivore production because the resulting crop of microbial biomass growing on D2 consists of compounds that are more easily absorbed and assimilated into biomass. Increasing λ , and hence microbial gardening, therefore serves to increase the gross growth efficiency of the detritivores (Fig. 2C). The benefits of gardening decline as D1 detritus becomes easier to absorb, i.e. its lability is increased (Fig. 2D). It ultimately becomes an adverse strategy when $\beta_1 \geq 0.3$. The utility of gardening will therefore vary in space, both vertically and horizontally, and also in time, depending on the numerous processes that influence the biochemical makeup of detritus.

Conclusions and prospects

Microbial gardening offers a potentially successful trophic strategy for zooplankton in the twilight zone of the ocean. It provides a source of easily digestible biomass that is rich in essential micronutrients. The model captures these benefits by assuming carbon gross growth efficiency increases when feeding on microbe-infested detritus. A more detailed analysis of this concept could in principle be carried out using a stoichiometric model with multiple currencies representing carbon and other nutritional factors. Taking into account both growth requirements and basal metabolic demands associated with tissue turnover, the limiting substrate can be identified, and growth predicted accordingly [49]. The conceptualisation of such models requires an understanding of the subject matter's physiology and empirical data for their parameterisation. In reality, we know little about the roles of micronutrients in deep-dwelling zooplankton or how they attain them.

We have much to learn about the biochemistry of different particle classes in the twilight zone, the physiological

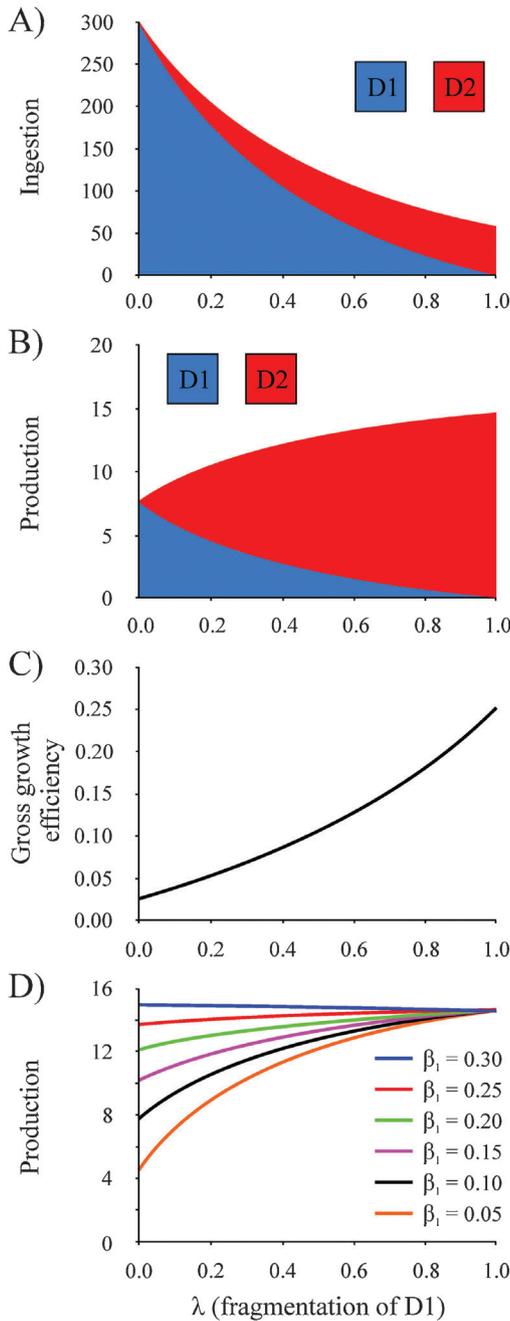


Figure 2. Model-predictions illustrating how the proportion of large, fast sinking particles (D1) fragmented into smaller, slow- or non-sinking particles (D2) by detritivorous zooplankton (λ) affects their: **A:** Ingestion, **B:** Production, **C:** Gross growth efficiency, and **D:** Production when the absorption efficiency of D1 particles (β_1) is varied. The complete budget is presented in Supporting Information Fig. S3. Ingestion and production (panels A, B, and D) are scaled to relative to a detrital flux of 100 (nominal units) entering the twilight zone.

adaptations that facilitate metazoan life in this environment and the ecological interactions that provision the resident organisms with the necessary biochemical compounds. Our ability to quantitatively understand the significance of

microbial gardening in the twilight zone, and the wider roles of the resident detritivorous zooplankton, requires more detailed knowledge of the food consumed by these animals, their basal metabolic demands, and the efficiencies

with which they absorb and assimilate elements and nutrients from their daily ration. These are not trivial challenges, given the small size of subject organisms and the potential for artefacts associated with capturing and removing them from their natural environment for experimentation. It is probable that a combination of in-situ preservation techniques, proxy-based estimates of physiology, and molecular tools, e.g. transcriptomics, proteomics, and metabolomics, will provide further insight into the role of zooplankton in the twilight zone.

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References

- Henson SA, Sanders R, Madsen E, Morris PJ, et al. 2011. A reduced estimate of the strength of the ocean’s biological carbon pump. *Geophys Res Lett* **38**: L04606.
- Kwon EY, Primeau F, Sarmiento JL. 2009. The impact of remineralization depth on the air-sea carbon balance. *Nat Geosci* **2**: 630–5.
- Turner JT. 2002. Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquat Microb Ecol* **27**: 57–102.
- Giering SLC, Sanders R, Lampitt RS, Anderson TR, et al. 2014. Reconciliation of the carbon budget in the ocean’s twilight zone. *Nature* **507**: 480–3.
- Steinberg DK, Cope JS, Wilson SE, Kobari T. 2008. A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean. *Deep-Sea Res II* **55**: 1615–35.
- Steinberg DK, Van Mooy BAS, Buesseler KO, Boyd PW, et al. 2008. Bacterial vs. zooplankton control of sinking particle flux in the ocean’s twilight zone. *Limnol Oceanogr* **53**: 1327–38.
- del Giorgio PA, Cole JJ. 1998. Bacterial growth efficiencies in natural aquatic systems. *Annu Rev Ecol Syst* **29**: 503–41.
- Straille D. 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnol Oceanogr* **42**: 1375–85.
- Wilson SE, Steinberg DK, Buesseler KO. 2008. Changes in fecal pellet characteristics with depth as indicators of zooplankton repackaging of particles in the mesopelagic zone of the subtropical and subarctic North Pacific Ocean. *Deep-Sea Res II* **55**: 1636–47.
- Fenchel T. 1970. Studies on the decomposition of organic detritus derived from the turtle

- grass *Thalassia testudinum*. *Limnol Oceanogr* **15**: 14–20.
11. **Hylleberg J.** 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. *Ophelia* **14**: 113–37.
 12. **Pond DW.** 2012. The physical properties of lipids and their role in controlling the distribution of zooplankton in the oceans. *J Plankt Res* **34**: 443–53.
 13. **Hazel JR, Williams EE.** 1990. The role of alterations in membrane lipid composition in enabling physiological adaptation of organisms to their physical environment. *Prog Lipid Res* **29**: 167–227.
 14. **Cossins AR, Macdonald AG.** 1986. Homeoviscous adaptation under pressure. III. The fatty acid composition of liver mitochondria phospholipids of deep-sea fish. *Biochim Biophys Acta* **860**: 325–35.
 15. **Lee RF, Hagen W, Kattner G.** 2006. Lipid storage in marine zooplankton. *Mar Ecol Prog Ser* **307**: 273–306.
 16. **Visser AW, Jonasdottir SHJ.** 1999. Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus*. *Fish Oceanogr* **8**: 100–6.
 17. **Mayor DJ, Cook K, Thornton B, Walsham P,** et al. 2011. Absorption efficiencies and basal turnover of C, N and fatty acids in a marine Calanoid copepod. *Funct Ecol* **25**: 509–18.
 18. **Clark KAJ, Brierley AS, Pond DW.** 2012. Composition of wax esters is linked to diapause behavior of *Calanus finmarchicus* in a sea loch environment. *Limnol Oceanogr* **57**: 65–75.
 19. **Pond DW, Tarling GA, Ward P, Mayor DJ.** 2012. Wax ester composition influences the diapause patterns in the copepod *Calanoides acutus*. *Deep-Sea Res II* **59–60**: 93–104.
 20. **Bell MV, Dick JR, Anderson TR, Pond DW.** 2007. Application of liposome and stable isotope tracer techniques to study polyunsaturated fatty acid biosynthesis in marine zooplankton. *J Plankt Res* **29**: 417–22.
 21. **Kattner G, Albers C, Graeve M, Schnack-Schiel SB.** 2003. Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: indication on feeding modes. *Polar Biol* **26**: 666–71.
 22. **Sano M, Maki K, Nishibe Y, Natata T,** et al. 2013. Feeding habits of mesopelagic copepods in Sagami Bay: Insights from integrative analysis. *Prog Oceanogr* **110**: 11–26.
 23. **Cowie GL, Hedges JL.** 1996. Digestion and alteration of the biochemical constituents of a diatom (*Thalassiosira weissflogii*) ingested by an herbivorous zooplankton (*Calanus pacificus*). *Limnol Oceanogr* **41**: 581–94.
 24. **de Baar HJW, Farrington JW, Wakeham SG.** 1983. Vertical flux of fatty acids in the North Atlantic Ocean. *J Mar Res* **41**: 19–41.
 25. **Fileman TW, Pond DW, Barlow RG, Mantoura RFC.** 1998. Vertical profiles of pigments, fatty acids and amino acids: Evidence for undegraded diatomaceous material sedimenting to the deep ocean in the Belling-shausen Sea, Antarctica. *Deep-Sea Res I* **45**: 333–46.
 26. **Lee C, Wakeham S, Arnosti C.** 2004. Organic matter in the sea: The composition conundrum. *Ambio* **33**: 565–75.
 27. **Pakulsky JD, Benner R.** 1994. Abundance and distribution of carbohydrates in the ocean. *Limnol Oceanogr* **39**: 930–40.
 28. **Boyd PW, Trull TW.** 2007. Understanding the export of biogenic particles in oceanic waters: Is there consensus? *Prog Oceanogr* **72**: 276–312.
 29. **Phillips NW.** 1984. Role of different microbes and substrates as potential suppliers of specific, essential nutrients to marine detritivores. *Bull Mar Sci* **35**: 283–98.
 30. **Leschine SB.** 1995. Cellulose degradation in anaerobic environments. *Annu Rev Microbiol* **49**: 399–426.
 31. **Plante CJ, Jumars PA, Baross JA.** 1990. Digestive associations between marine detritivores and bacteria. *Annu Rev Ecol Syst* **21**: 93–127.
 32. **König H, Varma A,** eds; 2006. *Intestinal Microorganisms of Termites and Other Invertebrates*. Berlin: Springer. p. 483.
 33. **Sochard MR, Wilson DF, Austin B, Colwell RR.** 1979. Bacteria associated with the surface and gut of marine copepods. *App Env Microbiol* **37**: 750–9.
 34. **Jøstensen J-P, Landfald B.** 1997. High prevalence of polyunsaturated-fatty-acid producing bacteria in arctic invertebrates. *FEMS Microbiol Lett* **151**: 95–101.
 35. **Dall W, Moriarty DJW.** 1983. Functional aspects of nutrition and digestion. In Mantel LH, ed; *The Biology of Crustacea vol 5. Internal Anatomy and Physiological Regulation*. Academic Press. p. 215–26.
 36. **Jackson GA.** 1993. Flux feeding as a mechanism for zooplankton grazing and its implications for vertical particle flux. *Limnol Oceanogr* **38**: 1328–31.
 37. **Lampitt RS, Noji T, von Bodungen B.** 1990. What happens to zooplankton faecal pellets? Implications for material flux. *Mar Biol* **104**: 15–23.
 38. **Noji TT, Estep KW, Macintyre F, Norrbin F.** 1991. Image analysis of faecal material grazed upon by three species of copepods: Evidence for coprophagy, coprophagy and coprochaly. *J Mar Biol Ass UK* **71**: 465–80.
 39. **González HE, Smetacek V.** 1994. The possible role of the cyclopoid copepod *Oithona* in retarding vertical flux of zooplankton faecal material. *Mar Ecol Prog Ser* **113**: 233–46.
 40. **Koski M, Kierboe T, Takahashi K.** 2005. Benthic life in the pelagic: Aggregate encounter and degradation rates by pelagic harpacticoid copepods. *Limnol Oceanogr* **50**: 1254–63.
 41. **Iversen MH, Poulsen LK.** 2007. Coprophagy, coprophagy, and coprochaly in the copepods *Calanus helgolandicus*, *Pseudocalanus elongatus*, and *Oithona similis*. *Mar Ecol Prog Ser* **360**: 79–89.
 42. **Fenchel TM, Jørgensen BB.** 1977. Detritus foodchains of aquatic ecosystems: The role of bacteria. *Adv Microbiol Ecol* **1**: 1–58.
 43. **Klein Breteler WCM, Schogt N, Baas M, Schouten S,** et al. 1999. Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. *Mar Biol* **135**: 191–8.
 44. **Parrish CC, French VM, Whitcar MJ.** 2012. Lipid class and fatty acid composition of copepods (*Calanus finmarchicus*, *C. glacialis*, *Pseudocalanus* sp., *Tisbe furcata* and *Nitokra lacustris*) fed various combinations of autotrophic and heterotrophic protists. *J Plankt Res* **34**: 356–75.
 45. **Aldredge A.** 1998. The carbon, nitrogen and mass content of marine snow as a function of aggregate size. *Deep-Sea Res I* **45**: 529–41.
 46. **Alonso-González IJ, Aristegui J, Lee C, Sanchez-Vidal A,** et al. 2010. Role of slowly settling particles in the ocean carbon cycle. *Geophys Res Lett* **37**: L13608.
 47. **Riley JS, Sanders R, Marsay C, Le Moigne FAC,** et al. 2012. The relative contribution of fast and slow sinking particle sin the ocean carbon export. *Glob Biogeochem Cycl* **26**: GB1026.
 48. **Calow P.** 1977. Conversion efficiencies in heterotrophic organisms. *Biol Rev* **52**: 385–409.
 49. **Mayor DJ, Anderson TR, Pond DW, Irigoien X.** 2009. Limitation of egg production in *Calanus finmarchicus* in the field: a stoichiometric analysis. *J Mar Sys* **78**: 511–7.