Carbon cycling and POC turnover in the mesopelagic zone of the ocean: Insights from a simple model

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Abstract. Carbon budgets of the mesopelagic zone are poorly constrained, highlighting our lack of understanding of the biota that inhabit this environment and their role in the cycling and sequestering of carbon in the deep ocean. A simple food web model of the mesopelagic zone is presented which traces the turnover of particulate organic carbon (POC), supplied as sinking detritus, through to its respiration by the biota via three pathways: colonization and solubilization of detritus by attached bacteria, production of free-living bacteria following losses of solubilization products during particle degradation, and consumption by detritivorous zooplankton. The relative consumption of detritus by attached bacteria was initially specified as 76%, with the remaining 24% by detritivores. Highlighting an asymmetry between consumption and respiration, the resulting predicted share of total respiration due to bacteria was 84.7%, with detritivores accounting for just 6.6% (with 6.5% and 2.2% by bacterivores and higher zooplankton respectively). Bacteria thus dominated respiration and thereby acted as the principal sink for POC supplied to the mesopelagic zone, whereas zooplankton mainly recycled carbon back to the base of the food web as detritus or dissolved organic carbon rather than respiring it to CO_2. Estimates of respiration are therefore not necessarily a reliable indicator of the relative roles of bacteria and zooplankton in consuming and processing POC in the mesopelagic zone of the ocean. The work highlighted a number of major unknowns, including how little we know in general about the dynamics and metabolic budgets of bacteria and zooplankton that inhabit the mesopelagic zone and, specifically, the degree to which the solubilized products of enzymatic hydrolysis of POC by attached bacteria are lost to the surrounding water, the

magnitude and factors responsible for bacterial growth efficiency, the role of microbes in the nutrition of detritivores, and the recycling processes by which zooplankton return what they consume to the food web as detritus and dissolved organic matter.

1. Introduction

Carbon produced by photosynthesis in the euphotic zone of the ocean is exported to deep waters via sinking particles, dissolved organic matter and migrating zooplankton, the so-called "biological pump" (Volk and Hoffert, 1985). This flux of organic carbon is then attenuated with depth, with the majority of consumption occurring within the so-called mesopelagic (or "twilight") zone, nominally assigned a depth range 100-1000 m. Our knowledge of processes occurring in this zone, and in particular the dynamics of the mesopelagic food web, is however restricted given the inherent difficulties of undertaking observational and experimental work in deep water. Modelers have therefore resorted to empiricism when describing the sinking of particles through the water column in ocean general circulation models, typically relying on simple curve fits of particulate organic carbon (POC) versus depth (e.g., Betzer et al., 1984; Martin et al., 1987; Pace et al., 1987). Without a mechanistic basis, however, this approach has its limitations, especially when it comes to predicting the response of, for example, the biological carbon pump to altered climate forcing.

The extent of our ignorance regarding processes in the mesopelagic zone is highlighted by carbon budgets that fail to reconcile the attenuation of POC with respiration by the food web (Burd et al., this issue). Boyd et al. (1999), for example, estimated that bacterial respiration was up to tenfold greater than POC supply in the mesopelagic zone of the subarctic Pacific. Similarly, Steinberg et al. (2008) calculated that the sum of respiration by bacteria and zooplankton between 150 and 1000 m at stations ALOHA (subtropical Pacific) and K2 (off Japan) exceeded the removal of sinking particles (estimated from POC as measured by neutrally buoyant sediment traps) by as much as an order of magnitude. Making progress to resolve these differences is far from straightforward given both the complex mixture of amorphous aggregates and fecal material that constitute POC (Fowler and Knauer, 1986) and the multitude of organisms in the mesopelagic food web that is driven by this supply of organic matter. Particles host

communities of microbes characterized by complex interactions among organisms that depend on rates of attachment, detachment, growth, mortality and intra- and interspecific competition for resources (Kiørboe et al., 2003). In turn, bacterial numbers are kept in check as flagellates rapidly colonize sinking aggregates (Caron, 1987; Artolozaga et al, 2002; Kiørboe et al., 2004). Utilization of POC by particle-attached bacteria requires the action of hydrolytic enzymes (Smith, et al. 1992), and it is commonly observed that attached bacteria have elevated enzymatic activities relative to their free-living counterparts (Grossart et al., 2003a; 2007). The recovery of the resulting dissolved organic substrates is however generally believed to be inefficient, with a significant proportion leaking to the surrounding water and supporting the production of free-living bacteria (Kiørboe and Jackson, 2001). Some zooplankton species can also directly feed on aggregates which are often broken up in the process (Lampitt et al., 1993; Dilling et al., 1998; Koski et al. 2005).

At the most basic level, there is little consensus even on the relative roles of bacteria and zooplankton as agents of turnover of POC in the mesopelagic zone of the ocean. The role of microbes was emphasized by Cho and Azam (1988) who postulated rapid solubilization of sinking organic particles by attached bacteria. Models have often followed suit. Boyd and Stevens (2002), for example, included an exponentially declining rate of microbial solubilization of particles with depth in their model of vertical flux of POC in the northeast Atlantic Ocean, but excluded zooplankton consumption of detritus. Their results indicated that downward transport is governed primarily by particle geometry, aggregation and microbial solubilization rates. On the other hand, Banse (1990) suggested that zooplankton may be primarily responsible for reducing particle flux with depth below the euphotic zone, estimating that grazers could account for 50 to 100% of the observed decline at two Pacific deep water stations. Other studies have similarly indicated the potential significance of zooplankton in the decomposition of snow particles (Green and Dagg, 1997; Steinberg et al., 1994). In total contrast to the model of Boyd and Stevens (2002) described above, Boehm and Grant (2001) used a model that included zooplankton grazing, sedimentation, coagulation and fragmentation, but which excluded microbial remineralization, and concluded that, at least in some instances, grazers may account for the diminution of biogenic carbon flux with depth. In

reality, both bacteria and zooplankton are likely important in POC turnover. In a modelling study of the northwest Mediterranean Sea, for example, Stemmann et al. (2004b) indicated that zooplankton are responsible for decreasing the flux of large particles in the upper mesopelagic zone, whereas microbial process become more important deeper in the water column as zooplankton become scarce in number.

The disparity in the various views among the scientific community regarding the relative roles of bacteria and zooplankton in POC turnover in the mesopelagic zone is worrisome, a state of affairs exacerbated by the contrasting assumptions used in apparently successful models. A central role of models is, after all, in providing explicit quantitative descriptions of what we do and do not understand (Gasol et al., 2008). With this in mind, we present here a simple food web model of the processes contributing to the attenuation of POC flux in the mesopelagic zone of the ocean. The model is a flow analysis, following turnover of organic carbon via attached microbial communities, bacteria free-living in the water column, detritivorous zooplankton and higher zooplankton. Our aim is not to make precise predictions of these various pathways constrained by data, but rather to explore the current state-of-the-art of our knowledge of the mesopelagic realm, highlighting key processes and areas of uncertainty that merit future research.

2. Model description

2.1. Structure and equations

The model presented here is a flow analysis that examines the role of bacteria and zooplankton in the consumption and remineralization of POC in the mesopelagic zone of the ocean. It has as its basis the model of Anderson and Ryabchenko (in press), in which detritus consumption in the mesopelagic zone of the Arabian Sea was partitioned between bacteria and zooplankton, with recycling of carbon via dissolved organic carbon (DOC) and higher predators. The representation of the mesopelagic food web in their model was however simplistic in that no distinction was made in terms of different groups of bacteria (e.g., attached, free-living) or zooplankton (e.g., bacterivores, detritivores and

higher zooplankton). The model of Anderson and Ryabchenko (in press) is elaborated here to provide a more detailed representation of carbon pathways within the mesopelagic food web by incorporating different groups of bacteria and zooplankton.

The starting point of the model is the net input of detritus into the mesopelagic zone via export from sinking particles, D_{EX}, representing the difference between detritus entering from above and that leaving at its base. The rate of diminution of POC with depth is not afforded an explicit treatment, rather the model operates on the basis that quantity D_{EX} of carbon is turned over within the mesopelagic layer, and traces the relevant pathways through bacteria and zooplankton leading to its ultimate respiration by the food web. Three food web pathways are considered (Figure 1): (1) detritus is colonized by attached bacteria and an associated bacterivore community; (2) detritivores consume detritus along with the associated microbial communities inhabiting it; (3) enzymatic hydrolysis by attached bacteria, as well as losses from zooplankton, releases DOC into the water column which fuels free-living bacteria and an associated microbial food chain. Free-living bacterivores and detritivores are consumed by higher zooplankton, which are ordered into an infinite chain. A list of model parameters is provided in Table 1.

Consumption of detritus is partitioned between attached bacteria (fraction ψ) and detritivores (1-ψ). Material acted on by attached bacteria is solubilized by hydrolytic enzymes (Smith et al., 1992) and the resulting release of organic carbon provides substrates not only for themselves, but also for free-living bacteria via loss of DOC to the surrounding medium (Cho and Azam, 1988; Karl et al., 1988). In the model, this loss of DOC is represented as fraction α of the POC acted upon by attached bacteria. The remainder is used for growth with efficiency ω_A (with 1-ω_A respired to CO_2), such that growth and respiration of attached bacteria, F_{BA} and R_{BA} respectively, are:

$$F_{BA} = \psi(1-\alpha)\omega_A D_T \tag{1}$$

$$R_{BA} = \psi(1-\alpha)(1-\omega_A)D_T \tag{2}$$

where D_T is total detritus within the system, including both net input from the euphotic zone (D_{EX}) and carbon produced as fecal pellets by the food web. Grazing is assumed to be the sole loss term for attached bacteria, either by detritivores consuming aggregates and associated microbes (fraction ζ) or by bacterivores in the particle-attached community ($1-\zeta$). A fraction, ϕ_V, of food material is released by bacterivores as DOC (incorporating losses such as sloppy feeding and excretion), and the remainder assimilated with efficiency β_V (with fraction $1-\beta_V$ lost as fecal material). Growth and respiration of attached bacterivores, F_{VA} and R_{VA}, are then calculated assuming a fixed net growth efficiency, k_V:

$$F_{VA} = (1-\zeta)F_{BA}(1-\phi_V)\beta_V k_V \tag{3}$$

$$R_{VA} = (1-\zeta)F_{BA}(1-\phi_V)\beta_V(1-k_V) + (1-\zeta)F_{VA} \tag{4}$$

As for attached bacteria, fraction ζ of bacterivores is assumed to be lost to consumption by detritivores, with the remainder assumed to contribute to respiration (model closure: the second term in Eq. 4).

Detritivorous zooplankton consume fraction $1-\psi$ of detritus in the model (food web pathway 2), along with fraction ζ of the community of attached bacteria and bacterivores inhabiting detrital particles. Fraction ϕ_H is released as DOC during grazing, with the remainder assimilated with efficiency β_H and used for growth with net growth efficiency k_H. Production and respiration of detritivores, F_H and R_H, are then:

$$F_H = (1-\phi_H)\beta_H k_H((1-\psi)D_T + \zeta(F_{BA}+F_{VA})) \tag{5}$$

$$R_H = (1-\phi_H)\beta_H(1-k_H)((1-\psi)D_T + \zeta(F_{BA}+F_{VA})) \tag{6}$$

The detritivore pathway is closed by an infinite chain of higher zooplankton. Fraction ϕ_Z is lost to DOC during transfer between trophic levels, and remaining food assimilated

with efficiency β_Z and used for growth with net growth efficiency k_Z. The summed production and respiration of this chain, F_{Z2} and R_{Z2}, are then:

$$F_{Z2} = F_H \sum_{i=1}^{\infty} [(1-\phi_Z)\beta_Z k_Z]^i = F_H(f[(1-\phi_Z)\beta_Z k_Z]-1) \tag{7}$$

$$R_{Z2} = F_H f[(1-\phi_Z)\beta_Z k_Z](1-\phi_Z)\beta_Z(1-k_Z) \tag{8}$$

where function f[x] is (e.g., Anderson and Ducklow, 2001):

$$f[x] = \sum_{i=0}^{\infty} x^i = \frac{1}{1-x}, \ 0 < x < 1 \tag{9}$$

The third food web pathway in the model, that of free-living bacteria and their associated food chain, is fuelled by supply of DOC. Supply from food web pathway 1 occurs via hydrolysis of POC by attached bacteria and from release of DOC by associated bacterivores, $J_{DOC,ex}$ and $J_{DOC,VA}$ respectively (normalized to detritus supply, D_T):

$$J_{DOC,ex} = \psi\alpha \tag{10}$$
$$J_{DOC,VA} = \psi(1-\alpha)\omega_A(1-\zeta)\phi_V \tag{11}$$

Similarly, DOC is supplied via detritivores and associated higher zooplankton in food web pathway 2, $J_{DOC,H}$ and $J_{DOC,HZ}$:

$$J_{DOC,H} = (1-\psi)\phi_H + \psi(1-\alpha)\omega_A\phi_H J_{H,BA} \tag{12}$$
$$J_{DOC,HZ} = \phi_Z(1-\psi)J_{Z,H} + \psi(1-\alpha)\omega_A\phi_Z J_{H,BA}J_{Z,H} \tag{13}$$

where $J_{H,BA}$ is the fraction of production by bacteria that is consumed by detritivores, including carbon in bacterivores one trophic level higher in the food chain, and $J_{Z,H}$ quantifies production of detritivores and associated higher zooplankton, normalized to the carbon input to food web pathway 2:

$$J_{H,BA} = \zeta + (1-\zeta)(1-\phi_V)\beta_V k_V \zeta \tag{14}$$

$$J_{Z,H} = (1-\phi_H)\beta_H k_H f[(1-\phi_Z)\beta_Z k_Z] \tag{15}$$

The total carbon supplied by food web pathways 1 and 2 that enters the DOC pool, $J_{DOC,D}$, is now:

$$J_{DOC,D} = J_{DOC,ex} + J_{DOC,VA} + J_{DOC,H} + J_{DOC,HZ} \tag{16}$$

As well as being responsible for turnover of DOC, the microbial loop (food web pathway 3) also acts as a source of dissolved material via free-living bacterivores and associated higher zooplankton, $J_{DOC,ML}$:

$$J_{DOC,ML} = J_{DOC,D} \sum_{i=1}^{\infty} (\omega_{FL} J_{DOC,BFL})^i \tag{17}$$

Here, $J_{DOC,BFL}$ is DOC produced by bacterivores and higher zooplankton per unit carbon entering pathway 3 during a single passage through the trophic levels, and the infinite summation term accounts for carbon cycling repeatedly around the loop.

$$J_{DOC,BFL} = \phi_V + \phi_Z J_{Z,V} \tag{18}$$

$$J_{Z,V} = (1-\phi_V)\beta_V k_V f[(1-\phi_Z)\beta_Z k_Z] \tag{19}$$

Production and respiration by free-living bacteria, F_{BFL} and R_{BFL}, are now calculated as:

$$F_{BFL} = \omega_{FL}(J_{DOC,D}+J_{DOC,ML})D_T = \omega_{FL}J_{DOC,D}f[\omega_{FL}J_{DOC,BFL}]D_T \tag{20}$$

$$R_{BFL} = (1-\omega_{FL})J_{DOC,D}f[\omega_{FL} J_{DOC,BFL}]D_T \tag{21}$$

Equations for the growth and respiration of bacterivores grazing on free-living bacteria, F_{VFL} and R_{VFL}, and the resulting chain of higher zooplankton, F_{Z3} and R_{Z3}, are:

$$F_{VFL} = F_{BFL}(1-\phi_V)\beta_V k_V \tag{22}$$

$$R_{VFL} = F_{BFL}(1-\phi_V)\beta_V(1-k_V) \tag{23}$$

$$F_{Z3} = F_{VFL}(f[(1-\phi_Z)\beta_Z k_Z]-1) \tag{24}$$

$$R_{Z3} = F_{VFL}f[(1-\phi_Z)\beta_Z k_Z](1-\phi_Z)\beta_Z(1-k_Z) \tag{25}$$

All that remains is to quantify D_T, the total consumption of detritus by the food web. For each unit of detritus entering food web pathways 1, 2 and 3, fractions J_{D1}, J_{D2} and J_{D3} are returned to the detritus pool as fecal material, rather than being released as DOC or respired as CO_2:

$$J_{D1} = \psi(1-\alpha)\omega_A((1-\phi_Z)(1-\beta_Z)J_{Z,H}J_{H,BA}+(1-\phi_H)(1-\beta_H)J_{H,BA}+(1-\zeta)(1-\phi_V)(1-\beta_V)) \tag{26}$$

$$J_{D2} = (1-\psi)((1-\phi_H)(1-\beta_H)+(1-\phi_Z)(1-\beta_Z)J_{Z,H}) \tag{27}$$

$$J_{D3} = \omega_{FL}J_{DOC,D}f[\omega_{FL}J_{DOC,BFL}]((1-\phi_V)(1-\beta_V)+(1-\phi_Z)(1-\beta_Z)J_{Z,V}) \tag{28}$$

The total carbon entering the detritus pool, D_T, is then calculated taking into consideration repeated cycling of organic matter within the food chain:

$$D_T = D_{EX}(1 + J_D + J_D^2 + J_D^3 + \ldots) = D_{EX}f[J_{D1}+J_{D2}+J_{D3}] \tag{29}$$

where J_D is the sum of J_{D1}, J_{D2} and J_{D3}.

2.2. Parameterization

The starting point of the flow analysis is to divide the utilization of POC supplied to the mesopelagic zone, D_{EX}, between attached bacteria (ψ) and detritivorous mesozooplankton (1-ψ). Assigning a value to this parameter is problematic given that the relative roles of bacteria and zooplankton in POC turnover by the mesopelagic food web are so poorly understood. Anderson and Ryabchenko (in press) estimated ψ using calculations of bacterial and zooplankton consumption of POC between 150 and 1000 m at stations ALOHA (22º 45'N, 158 ºW) and K2 (47 ºN, 160 ºE) provided by Steinberg et al. (2008). The average ratio of bacterial production to zooplankton respiration at the two sites was 0.75. Anderson and Ryabchenko (in press) tuned parameter ψ to give this ratio in their model, giving $\psi = 0.76$, i.e., indicating that 76% of particle consumption was carried out by bacteria and 24% by zooplankton. We use $\psi = 0.76$ here, but will examine model sensitivity to this parameter.

Another difficult parameter to quantify is α, the fraction of detritus turnover due to attached bacteria that is lost as DOC to the free-living bacteria food chain (pathway 3, Figure 1). Many investigators have suggested that most of the hydrolytic products of attached bacteria are lost to the surrounding water, thereby fuelling growth of their free-living counterparts (Cho and Azam, 1988; Smith et al., 1992; Grossart and Simon, 1998; Unanue et al., 1998). Cell-specific enzymatic activity of attached bacteria is usually at least an order of magnitude higher than that of free-living bacteria (Grossart et al. 2007), supporting the hypothesis that attached bacteria solubilize detrital material faster than they are able to take up the resulting products and leading to significant leakage of DOC that can be exploited by free-living bacteria. Further, deep water prokaryotes express more extracellular enzymes per cell than those in surface water (Baltar et al., in press). Vetter et al. (1998) undertook a modeling study that provided a cost-benefit analysis of attached bacteria in terms of quantities of enzyme release. Results suggested that enzymatic activity by bacteria on particle aggregates usually causes solubilization one to two orders of magnitude greater than the uptake of hydrolysate by the bacteria. Substrate quality likely affects solubilization losses. Smith et al. (1992), for example, found that leakage of dissolved combined amino acids varied with the type of detritus with release

of 95-98%, 98% and 50% from larvacean houses, diatom aggregates and fecal pellets respectively. It should be noted, however, that Smith et al. (1992) sampled relatively fresh detritus from the upper 25 m of the water column. The residence time of detrital material within the mesopelagic zone is at least several days, even if sinking rate is as high as 150 m d^{-1} (Shanks 2002), by which time all the detritus-bound amino acids would have been lost if aggregates comprise only fresh material. The degree of leakage is likely to decrease as the detritus ages in the mesopelagic zone. Grossart and Ploug (2001), for example, detected enzymatic activity and production of attached bacteria on old aggregates, albeit at much reduced rates. They estimated that 26% of the POC and >50% of the particulate combined amino acids (PCAA) of aggregates were successfully taken up by attached bacteria, much higher than the estimates of Smith et al. (1992). In similar fashion, Müller-Niklas et al. (1994) also reported a tight coupling between attached bacterial production and enzymatic activity on amorphous aggregates collected from the northern Adriatic Sea, contradicting the idea of loose coupling between hydrolysis of detritus and DOC uptake by attached bacteria. Accordingly, we may expect that α is much less than a value of 0.9 that might be expected for fresh aggregates, and instead chose a more conservative value of 0.5 for our standard run of the model.

The available evidence points to bacterial growth efficiency (BGE) in the ocean being low. In their review of the literature, del Giorgio and Cole (1998) indicated a mean oceanic BGE of 0.15. What values might be expected for particle-attached and free-living bacteria in the mesopelagic zone? Two (partially related) factors are of importance, namely the cost of enzyme synthesis and the quality of the substrate. Regarding the former, the activity of hydrolytic enzymes can increase by 10 fold or more when bacteria move out of solution and attach to particles (Grossart et al. 2007) which, if these enzymes are a significant fraction of the total proteins produced by the cell, would suggest that BGE should accordingly be reduced because of the associated cost of synthesis (Vetter et al., 1998). Conversely, higher BGEs may be associated with fresh labile material in particles rapidly exported from the euphotic zone. Grossart and Ploug (2000) recorded a BGE of 0.45 for aggregate-associated bacteria during the first 3 days of colonization, subsequently declining to 0.23 and 0.04 after 7 and 14 days, respectively. These values are higher than the BGEs of between 0.09 and 0.17 estimated by Smith et al. (1995) for

bacteria growing on 1-3 day old aggregates produced during the breakdown of a diatom bloom. We are restricted to using a single value for the BGE of attached bacteria in our flow analysis, and chose to use $\omega_A = 0.24$ which is the mean of the three values given in Grossart and Ploug (2000) corresponding to measurements on days 1-3, 7 and 14. Estimates of BGE for bacteria growing on laboratory-generated diatom aggregates are similar in magnitude, e.g. 0.1-0.5, mean 0.26 (Ploug and Grossart, 2000) and 0.23 (old aggregates: Grossart and Ploug, 2001). BGEs of between 0.10 and 0.21 were recorded by Panagiotopoulos et al. (2002) during in vitro incubation experiments examining the degradation of large particles in the southern Indian Ocean. In the case of free-living bacteria, one might expect a relatively low BGE in the mesopelagic zone given that BGE varies systematically with bacterial production and the trophic richness of ecosystems, with lowest values in the most dilute oligotrophic systems (Del Giorgio and Cole, 1998). We chose to use $\omega_{FL} = 0.15$, equal to the mean ocean value calculated by del Giorgio and Cole (1998), although recognizing that in actuality BGE in the mesopelagic zone may be even lower.

Grazing is a major process in the model, both by bacterivores on attached and free-living bacteria, as well as by detritivores and higher zooplankton. Parameters ϕ_V, ϕ_H and ϕ_Z express the fractions of grazed material lost to DOC during each trophic transfer. The mechanisms of this release of DOC are break up of food while feeding (so-called "sloppy feeding"), excretion, and voiding of feces with loss of included dissolved matter (Jumars et al., 1989). Strom et al. (1997) found in laboratory experiments that heterotrophic protists and copepods released 16-37% of their ingestion as DOC. Heterotrophic flagellates use a variety of mechanisms, including pallium feeding, tube feeding and direct engulfment (Hansen and Calado, 1999; Montagnes et al., 2008), which likely entail negligible sloppy feeding losses because prey are ingested whole or have their constituents sucked out. DOC is however released by flagellates, possibly as loss of their own digestive enzymes and incompletely digested membranes as well as other cellular components from the prey (Nagata and Kirchman, 1992). We set $\phi_V = 0.25$, the fraction of uptake by flagellates excreted as organic matter in the model of the microbial food web of Blackburn et al. (1997). Regarding mesozooplankton, Copping and Lorenzen (1980) found that DOC released by *Calanus pacificus* was 27% of grazed material when

fed phytoplankton in the laboratory. A much higher value of 43% was estimated by Møller et al. (2003) for *Calanus* spp. feeding on diatoms (excluding 6% leakage from fecal pellets that may be atypically high because of rapid gut passage times under high food concentration condition in their experiment). For higher zooplankton, we set ϕ_Z = 0.3, the same value used by Anderson and Ducklow (2001). We can safely assume that sloppy feeding is even more likely in the case of detritivores because fecal pellets and aggregates are large and fragile (Møller et al., 2003). We therefore set ϕ_H = 0.4.

Remaining grazed material is subject to assimilation before being utilized for growth. The fraction of carbon egested by flagellates varies between 13 and 44% (Fenchel, 1982; Geider and Leadbeater, 1988; Pelegrí et al., 1999). Using an average of these two values gives an assimilation efficiency, parameter β_V, of 0.72. Anderson (1994) developed a model relating C:N ratios in mesozooplankton food and the resulting fecal pellets in which different carbon fractions (lipids, carbohydrates, proteins) were assigned different assimilation efficiencies based on the data of Head (1992) for copepods off the coast of Labrador and in the Gulf of St. Lawrence. Fresh diatoms with a C:N ratio of 6.5 (with C content 61% protein, 12% lipid and 27% carbohydrate) were assimilated with an average efficiency of 0.66, and so this value was assigned to parameter β_Z. Material that had passed through the gut once, i.e. pellet material, was assimilated with efficiency 0.60, giving β_H = 0.60. The recalcitrant nature of most detrital material means that relatively low assimilation efficiencies are to be expected in detritivorous food chains (Chervin, 1978; Anderson et al., 2004).

Assimilated carbon is used by zooplankton for growth, with the remainder being respired as CO_2. Based on a review of the literature, Straile (1997) calculated average gross growth efficiencies (GGEs) for flagellates and copepods of 0.32 and 0.26 respectively. These values can be converted to net growth efficiency (NGE), i.e. the fraction of assimilated carbon converted to biomass, by dividing by assimilation efficiency (β_V and β_Z), yielding 0.44 and 0.39 for flagellates and copepods respectively. The former value, from which we set k_V = 0.44, is similar to the NGE of 0.4 estimated for flagellates by Pelegrí et al. (1999). For simplicity, we set both k_H and k_Z to 0.39. Detritivores tend to have significantly lower carbon GGE than herbivores and predators (Frost et al., 2006), but this may be largely a result of the lower assimilation efficiencies,

which have no effect on NGE. It is possible that limitation by nutrient elements in food may put severe constraints on detritivores (Cross et al., 2003), negatively impacting production efficiency, but the same is also likely the case for herbivorous mesozooplankton (Kuijper et al., 2004).

Finally, parameter ζ specifies the fraction of the attached bacteria and bacterivore community that is consumed by detritivores. There is little empirical evidence to help with setting a value for this parameter. For simplicity, we assumed that this partitioning is the same as the partitioning of detritus between bacteria and zooplankton, and thereby set $\zeta = 1-\psi = 0.24$. The model is not sensitive to this parameter.

The equations presented above provide a steady state solution to carbon cycling by the mesopelagic food web. As a first approximation, it is probably reasonable to assume that the mesopelagic zone is in steady state although, for some ocean regions such as the Arabian Sea where lateral transports are significant, it is necessary to consider timescales of ocean physics and their interaction with the biota (Burd et al., this issue).

The model was implemented in Microsoft Excel, and is available on request from the first author.

3. Results

Fluxes associated with the cycling of POC through to its ultimate respiration by the mesopelagic food web, as predicted by the model with default parameter settings (Table 1), are shown in Figure 2. Attached and free-living bacteria are each responsible for 38% of detritus turnover (indirectly via solubilization to DOC in the case of the latter), which includes POC supplied from the euphotic zone and an additional 13% from the production of fecal material *in situ* by zooplankton within the mesopelagic zone. Zooplankton account for the remaining 24% of detritus turnover. A considerable proportion of the carbon processed by the food web is cycled via DOC, which is generated either by the action of hydrolytic enzymes produced by particle-attached bacteria on detritus (70% of DOC production), or by release of DOC by grazers (30%). The ultimate fate of carbon supplied as POC from the euphotic zone is respiration by the

mesopelagic food web, in addition to flux out of the base of the mesopelagic zone (which is included implicitly within D_{EX}). Bacteria are predicted to account for 84.7% of total respiration (32.5% and 52.2% from attached and free-living bacteria), relatively higher than their contribution to consumption of POC (76%) because of their low growth efficiency and the fact that bacteria are the sole users of DOC recycled within the food web. Of the 15.3% contribution to total respiration by zooplankton in the model, only 6.6% is due to detritivores, remarkably lower than their 24% contribution to detritus consumption. The other 6.5% and 2.2% are contributed by bacterivores and higher zooplankton, respectively. The relatively low contribution of detritivores to food web respiration occurs because only 22% of what they consume is respired, while 40% is released as DOC, 24% lost as pellets and 14% incorporated into biomass. Results thus demonstrate a marked asymmetry between bacteria and zooplankton in their relative contributions to detritus consumption and total respiration.

Total production of the mesopelagic ecosystem as predicted by the model is low because of the low growth efficiencies of the organisms involved. Production by attached and free-living bacteria, normalized to D_{EX}, are 0.10 and 0.092 respectively, with incorporation of just 0.042, 0.040 and 0.014 for detritivores, bacterivores and higher zooplankton. Attached bacteria and bacterivores were predicted to contribute only 9.7% to the diet of detritivores. The microbial food web thus appears to be a sink for organic matter in the mesopelagic zone, with relatively little carbon being incorporated into bacterial biomass let alone higher trophic levels.

A sensitivity analysis was undertaken of the effect of altering parameter values on the relative contributions of different organisms to the consumption of detritus, as well as production and respiration by the food web (Figure 3). The greatest changes in consumption and respiration are seen by altering parameters ψ and α. Indeed, the asymmetry between these two processes becomes even more exaggerated if the zooplankton share of detritus consumption is increased by decreasing the value of parameter ψ. If, for example, the relative contributions of bacteria and zooplankton are made equal by setting $\psi = 0.5$ then, although detritivores directly consume half the detritus in the system, they account for just 13.8% of total respiration (with bacteria, bacterivores and higher zooplankton accounting for 76.9%, 5.5% and 3.8% respectively).

Going yet further and reversing the relative contributions of bacteria and zooplankton by setting $\psi = 0.24$ leads to an even more extreme mismatch with detritivores accounting for 76% of detritus consumption, but just 22.2% of total respiration.

Varying parameter α, the fraction of POC solubilized by attached bacteria that leaks to the surrounding water and which fuels the growth of free-living bacteria, directly affects the relative contributions of these two groups of microbes as regards processing of carbon by the food web, but has little impact on the overall balance of respiration between bacteria in total versus that of zooplankton. Slightly more carbon is predicted to reach higher trophic levels if attached bacteria are relatively dominant (low α) because of their greater BGE. Increasing ω_A by 50% (from 0.24 to 0.36), for example, gives rise to an increase in the production of attached bacteria of 52.0%, yet a decrease in their respiration of just 14.7%. Increasing ω_{FL} by 50% (from 0.15 to 0.225) increases production of free-living bacteria by 56.3%, with a corresponding decrease in respiration of just 5.0%. Even if this parameter is given a more extreme setting of 0.6 (an increase of 300%), production increases by over 427% and yet respiration decreases by only 38.0%. Thus, the role of microbes as the dominant sink for carbon in the food web is relatively insensitive to the microbes' growth efficiency.

Finally, the overall balance of respiration was relatively unaffected by parameters for zooplankton although production, and therefore potential transfer to higher trophic levels, was significantly increased by decreasing ϕ, increasing β or increasing k (note that, for ease of interpretation, parameters were varied simultaneously for each of the three zooplankton groups, detritivores, bacterivores, and higher predators). The relative contribution of zooplankton to respiration is increased by decreasing their resupply of carbon to the food web via DOC and fecal pellets, but the overall effect was small. For example, decreasing parameters ϕ and β by 50 and 25% respectively led to decreases in the bacteria share of total respiration from 84.7% to 79.9 and 80.9% respectively. Likewise, the model is insensitive to parameter ζ, which quantifies the grazing of attached bacteria and bacterivores by detritivores (not shown). Although it is impossible to exhaustively examine sensitivity in multidimensional parameter space, our findings appear to be generally robust to choice of parameter values.

4. Discussion

4.1 Sources and sinks of C in the mesopelagic zone

Attempts to budget carbon in the mesopelagic zone by comparing estimates of POC supply and respiration by the food web have generally shown large imbalances, highlighting our ignorance of remineralization pathways and compromising the construction of models to predict sequestration of carbon in the ocean (Burd et al., this issue). At the most basic level, the relative contributions of the two main groups of organisms, bacteria and zooplankton, in the turnover of POC remain poorly understood. Various studies have found that the carbon demand of bacteria alone falls short of the supply of POC from the euphotic zone (Ducklow, 1993; Turley and Mackie, 1994; Nagata et al., 2001; Baltar et al., 2009). Others have attempted to reconcile the combined carbon demands of bacteria and zooplankton with the diminution of POC flux in the mesopelagic zone. Steinberg et al. (2008), for example, estimated that bacterial carbon demand in the mesopelagic zone (150-1000 m) was 3- to 4-fold (station ALOHA) and 10-fold (K2) greater than the POC supply, while the carbon demand of zooplankton was 1-2 fold (ALOHA) and 3-9 fold (K2) greater. Anderson and Ryabchenko (in press) estimated that bacteria and zooplankton accounted for 82% and 18% of particle flux respectively in the mesopelagic zone of the Arabian Sea, but also concluded that the total carbon demand of the biota was significantly in excess of carbon supply. Findings such as these led Burd et al. (this issue) to ask: "What the @$#! is wrong with present calculations of carbon budgets?".

Here, we examined the balance between POC supply and respiration by bacteria and zooplankton using a simple flow analysis of the mesopelagic food web. The starting point was to divide detritus consumption between attached bacteria and detritivorous zooplankton (parameter ψ). One approach is to assume that bacteria account for most of this consumption. Indeed, the apparent dominance of microorganisms in the turnover of POC below the euphotic zone has generally prevailed as conventional wisdom, e.g., "The flux of organic matter decreases strongly with depth in oceanic water columns, reflecting microbial remineralization" (Fenchel et al., 2000). The role of zooplankton should not

however be discounted. Although there exist many qualitative reports of zooplankton colonizing and consuming detritus (e.g., Shanks and Edmondson 1990; Steinberg, 1995; Green and Dagg, 1997), quantitative estimates of the resulting degradation rates of POC are rare and highly variable, ranging between <0.1% and 91% d^{-1} (Koski et al. 2007). The extent of detritivory is likely species specific as some zooplankton species, such as the copepods *Oithona* spp., *Oncaea* spp. and *Microsetella* spp., are frequently found concentrated around detritus (Steinberg et al., 1994; Green and Dagg, 1997). Koski et al. (2005) estimated that the fraction of detrital aggregates (phytoplankton and other microbes) consumed by *Microsetella norvegica* is a function of aggregate size and copepod abundance. Using their field data, we estimated that even at the reported maximum *in situ* abundances, *M. norvegica* would consume 20% or less of the available detrital aggregates. Similarly, Koski et al. (2007) estimated that the zooplankton community consumes less than 30% of discarded larvacean houses within the upper 50 m. In a recent experimental study, Poulsen and Kiørboe (2005) estimated that only 5% of the fecal pellets encountered by epipelagic copepods were actually ingested. Using field measurements, these authors likewise found that mesozooplankton consumed an insignificant fraction of the fecal pellets in the North Sea (Poulsen and Kiørboe, 2006). We set $\psi = 0.76$, i.e. indicating that attached bacteria were responsible for 76% of detritus consumption, with 24% by detritivorous zooplankton, based on the model of Anderson and Ryabchenko (in press). Overall, we believe that this parameter setting is reasonable but note that, because the ratio of detritus consumed by bacteria and zooplankton is a fixed parameter in the model rather than an emergent property, we make no claim to have constrained it using the analysis.

In the model, bacteria account for a dominant 84.7% share of total respiration (32.5% and 52.2% from attached and free-living bacteria respectively), greater than their 76% contribution to POC consumption. Detritivores contribute just 6.6% toward total respiration, despite consuming 24% of POC, with the remaining respiration divided between bacterivores (6.5%) and higher zooplankton (2.2%). Growth efficiencies are low for organisms in the mesopelagic food web, notably the bacteria, hence the low transfer of carbon to bacterivores and higher zooplankton. Even if the relative roles of bacteria and zooplankton in consumption of POC are reversed by setting $\psi = 0.24$, detritivores

account for only 22.2% of respiration despite being responsible for 76% of POC turnover. At first sight, results appear to be consistent with the conventional view of the microbial loop as a sink for carbon because it includes several trophic levels such that most organic carbon is dissipated as CO_2 (Fenchel, 2008). Matters are however more complicated here because bacteria are predicted to dominate food web respiration even if detritivorous zooplankton are responsible for consuming much of the POC. Zooplankton in the model acted primarily as recyclers of carbon to the base of the food web as fecal pellets or DOC, rather than as a carbon sink through respiration. Of the material that detritivores consumed, just 22% is respired which at first sight is surprising given that gross growth efficiencies of zooplankton are usually low (Straile, 1997). In fact, the growth efficiency of detritivores is low in the model, but rather than being respired, most carbon is recycled back to the food web as DOC (40%) and fecal pellets (24%), with just 14% utilized for growth. The model thus indicates that bacteria dominate respiration in the mesopelagic zone and zooplankton act primarily to recycle carbon as detritus and DOC. This conclusion, which was remarkably robust to parameter sensitivity analysis (Figure 3), implies that estimates of respiration are not necessarily reliable indicators of the relative roles of bacteria and zooplankton in consuming POC in the mesopelagic zone of the ocean.

POC provides the sole supply of carbon in the model, which is then processed by the food web and ultimately respired by bacteria or zooplankton. There are however various other potentially significant sources of carbon to the mesopelagic zone (for a more extensive treatment, see Burd et al., this issue). Convective mixing of DOC from the euphotic zone is one additional source of carbon which may support 10% of heterotrophic metabolism below 500 m (Arístegui et al., 2002). DOC, as well as fecal pellets, could also be supplied to the mesopelagic zone by vertically migrating zooplankton (Banse, 1990). Estimates indicate that between 15 and 50% of zooplankton biomass above 500 m migrates downward during the day (Honjo et al., 2008 and references therein), excreting labile organic carbon that becomes available for microbes in deep water (Doval and Hansell, 2000). Vertical migrators were suggested by Steinberg et al. (2008) as a possible missing term in current estimates of the carbon budget of the mesopelagic zone. If included in our model, these sources of organic matter would

increase the size of the microbial sink for carbon, further exaggerating the primacy of bacteria over zooplankton as the ultimate fate of carbon in the system.

An intriguing source of organic carbon to the mesopelagic zone that might be considerably more important than hitherto assumed is chemoautotrophy, particularly by marine Crenarchaeota (Francis et al., 2005; Ingalls et al., 2006). These prokaryotes fix CO_2 using oxidation of ammonia as an energy source, with the resulting production of organic carbon being as much as 1 mmol C m^{-2} d^{-1} (Herndl et al., 2005). The extent to which this source of organic carbon drives the mesopelagic food web remains to be determined (Herndl et al., 2008).

4.2 Carbon cycling by the mesopelagic food web

The model indicates that zooplankton recycle most of the carbon that they process as fecal pellets or DOC. A similar conclusion was reached by Xu and Wang (2003) who studied the fate of diatom carbon when grazed by subtropical copepods, their results indicating the role of zooplankton in recycling organic matter in the ocean, particularly as DOC. High recycling in the model was due to low assimilation efficiencies (β_H and β_Z of 0.60 and 0.66) and high release of DOC during grazing (ϕ_H and ϕ_Z of 0.4 and 0.3) by zooplankton (see section 2, the model description, for justification of parameter values). These combinations of parameters led to detritivores and higher zooplankton respiring just 22% and 28% of the material they consume. Is this realistic? Complete metabolic budgets of organisms, in which measurements of respiration and intake are compared, are rare, particularly in the contemporary literature. Early studies with copepods by Copping and Lorenzen (1980) and Abou Debs (1984) indicated respiration losses as a fraction of intake of 7-10% and 20% respectively. More recently, Thor et al. (2002) found that respiration by *Acartia tonsa* could be as much as an order of magnitude lower than intake of different algal diets. Conversely, Mayzaud et al. (2002) measured respiration rates in five Southern Ocean copepods and found that they varied from 50% to 255% of ingestion. Xu and Wang (2003) noted that respiration was 21-56% in the copepod *Acartia spinicauda*. Estimates of respiration are known to vary according to experimental protocols (temperature, degree of acclimation, etc.). Respiration also depends on food

quantity (Bohrer and Lampert, 1988), as well as stoichiometric constraints on metabolic budgets (Anderson et al., 2005). Zooplankton consuming a diet rich in carbon, as might be expected for detritus, may be limited by nutrient elements, in which case they must dispose of the excess carbon (Hessen and Anderson, 2008). One option is to respire it (e.g. Anderson et al., 2005), although zooplankton may instead release it as DOC (Darchambeau et al., 2003; Jensen et al., 2006). Further studies are required in order to provide improved metabolic budgets of zooplankton.

The extent to which zooplankton influence the downward passage of sinking particles is notable given that they apparently are second to the microbes when acting as agents of POC turnover. They are key players in modifying this flux as it descends through the water column, both by repackaging food items into fecal pellets (Wilson et al., 2009) and in the disaggregation and fragmentation of particles (Dilling and Alldredge, 2000; Iversen and Poulsen, 2007). Lampitt et al. (1991), for example, reported that copepods break up their own pellets when attempting to ingest the contents, a wasteful process that they named "coprorhexy". Modeling studies have suggested that zooplankton likely play a major role in consuming the large particles that occur in the upper mesopelagic zone, whereas bacteria are responsible for degradation of the smaller, more recalcitrant particles that are present further down the water column (Jackson and Burd, 2002; Stemmann et al., 2004b). A further consideration is that, in addition to copepods, the mesopelagic food web contains all manner of "lurkers of the deep" such as appendicularians, siphonophores, fish and squid (Robison, 1978, 2004). While these animals may contribute little to overall respiration, their wide diversity in function makes predicting their impact on particle flux through the mesopelagic zone a particularly difficult challenge.

The role of zooplankton in detrital food webs is not well understood (Artolozaga et al., 2002). Microzooplankton are known to be efficient bacterivores (Zubkov and Sleigh, 2000; Kiørboe et al., 2004), and indeed in the model it was assumed that bacteria were their sole source of nutrition. As microbial biomass is small relative to that of the detritus they colonize, it may be that bacterivores also consume some of the aggregate material, particularly if it contains relatively fresh algal matter (Simon et al., 2002). The extent to which microzooplankton associated with particles are selective in their feeding is

however unclear. On the one hand, some species of flagellates and ciliates have become specialized to feed on bacteria inside aggregates (Caron, 1987). On the other, particles may serve as a refuge for bacteria and, further, a number of species exist that cannot be readily ingested due to their morphology (Jürgens and Güde, 1994). Bacteria attached to particles can also be consumed by larger zooplankton (Schoenberg and Maccubbin, 1985; Lawrence et al., 1993), although the overall contribution of microbes to animal nutrition may only be small (Baker and Bradnam, 1976). In the model, bacteria, along with associated bacterivores, contributed only 9.7% of detritivore diet in terms of carbon. The ability to consume different kinds of food is nevertheless important in achieving a nutritionally replete ration (Kleppel, 1993). Bacteria may provide an important source of nitrogen and phosphorus, as well as essential compounds such as amino and fatty acids, and their role in the nutrition of detritivores should therefore not be underestimated.

Microbial processes lie at the heart of the model, with bacteria dominating food web respiration. A key unknown is the extent to which POC solubilized by hydrolytic enzymes produced by attached bacteria is lost to the surrounding water. High losses of solubilized products have been suggested (Cho and Azam, 1988; Smith et al., 1992; Grossart and Simon, 1998; Unanue et al., 1998), but it may be that these are most applicable to fresh detritus and that losses associated with older aggregate material are lower. A 50% loss of solubilized products to the surrounding water was assigned in the model ($\alpha = 0.5$), leading to attached and free-living bacteria accounting for 32.5% and 52.2% of total respiration (greater in the latter because of the lower growth efficiency of free-living bacteria, 0.15 versus 0.24). Production of the two groups was predicted to be similar, 0.10 and 0.092 (normalized to D_{EX}) for attached and free-living bacteria respectively. In this regard, the lower growth efficiency of free-living bacteria was offset by the greater recycling of carbon as DOC (relative to detritus) in the system. Observations have generally suggested that the contribution of attached bacteria to total bacterial production is < 5 to 15% (Iriberri et al., 1990; Turley and Mackie, 1994), largely due to the fact that free-living bacteria are much more abundant than attached bacteria. Because total bacterial production in our model is ultimately constrained by detritus input from the euphotic zone, the discrepancy between model predictions and observations in term of attached vs. free-living bacterial production can be partly explained by release of

progeny by attached bacteria to the ambient water (Jacobsen and Azam, 1984; Batty et al., 2000), and additional sources of DOC (discussed in section 4.1) that are used primarily by free-living bacteria. The model highlights the need for improved estimates of, and understanding of, BGE in aquatic systems. One problem that, for example, arises when measuring BGEs of bacteria from deep water is decompression, which tends to induce increased energy costs and so leads to underestimates of this quantity (Tamburini et al., 2003).

The fate of bacteria in marine systems, and particularly the mesopelagic zone, is another subject of debate. Bacterivory is the obvious sink term. Virus induced mortality may occasionally be as important as grazing in the removal of bacteria, particularly under eutrophic conditions (Fuhrman and Noble, 1995; Weinbauer and Peduzzi, 1995), but less so when nutrients are scarce. Weinbauer et al. (2003), for example, estimated that viruses were responsible for only 3-5% of bacterial mortality in the mesopelagic waters of the Mediterranean Sea. In contrast, Tanaka et al. (2005) suggested that virus induced mortality of bacteria in the mesopelagic layer could be similar to or greater than that by heterotrophic nanoflagellates using a steady state food chain model. The fate of bacteria inhabiting the nutritionally dilute environment away from particles is unclear, especially as they appear able to withstand prolonged periods of starvation (Jones and Rhodes-Roberts, 1981; Kurath and Morita, 1983), although starvation does reduce the motility of bacteria and the rate at which they colonize aggregates (Yam and Tang, 2007). Lysis products as a result of mortality induced by viruses likely contribute to the pool of DOC, thereby sustaining further microbial uptake (Noble and Fuhrman, 1999; Middelboe and Lyck, 2002). This "viral loop" (Bratbak et al., 1992) thus prevents organic carbon reaching higher trophic levels such that if lysis was added to our model, it would have served to further strengthen the already dominant microbial sink for carbon.

A further complication regarding the role of microbes in carbon cycling in the mesopelagic zone is that the distinction between attached and free-living bacteria is not clear cut. Many marine bacteria are motile, exhibiting chemotactic behaviour that allows them to cluster around patches of dissolved organic matter or to rapidly colonize sinking particles (Grossart et al., 2003b, 2007). During the early age of a detritus particle a bacterium may attach and detach repeatedly, leading to an active exchange of bacteria

between the "attached" population and the "free-living" population (Kiørboe et al. 2002). As a result, free-living bacteria may inhabit the microzones of organic enrichment that surround particles, the so-called detritosphere (Biddanda and Pomeroy, 1988) rather than the barren aqueous environment in between. We are not suggesting that attached and free-living bacteria are one and the same within the confines of the detritosphere, as the two groups appear to be phylogenetically distinct (DeLong et al., 1993). A permanently attached and increasingly specialized bacteria population will establish as particles age (Grossart et al. 2006). Further work is needed to understand the consequences of changing microbial diversity on and around detritus particles in terms of carbon cycling in the mesopelagic zone (Robinson et al., this issue).

4.3 Concluding remarks

A great advantage of models is that they offer a framework in which the ramifications of existing knowledge can be articulated, and from which novel predictions can be made (Anderson, in press). We developed a simple food web model in order to study carbon cycling by the mesopelagic food web, highlighting areas that merit further research. The major conclusion of the work is that respiration by bacteria is the dominant sink for organic carbon in the mesopelagic zone, with zooplankton acting primarily to recycle material back to the base of the food web as fecal pellets and DOC. This asymmetry urges caution when using estimates of respiration by bacteria and zooplankton to infer the relative roles of these two groups of organisms in processing and recycling carbon in the mesopelagic zone. An advantage of the model is its simplicity. Results were shown to be robust with respect to the limited number of parameters, the dominance of the microbial sink for carbon being insensitive to whether bacteria or zooplankton are the major consumers of POC and to chosen values for BGEs. The model highlights how little is known about the mesopelagic food web, and in particular the relative roles of bacteria and zooplankton in consuming detritus, the degree to which the solubilized products of enzymatic hydrolysis of POC by attached bacteria are lost to the surrounding water, the magnitude and factors responsible for BGE, the role of microbes in the nutrition of detritivorous zooplankton, and metabolic budgets of zooplankton and

the extent to which these animals respire what they consume or return it to the food web as detritus or dissolved organic matter.

Simple models such as the one presented here are ideal for helping to focus our attention on the different aspects of carbon cycling in the mesopelagic food web. There are however limits to what can be deduced, with a need to complement these with more complex models (e.g. Jackson and Burd, 2002; Stemmann et al., 2004 a,b; Jackson et al., 2005) that address in greater detail the structure of the mesopelagic food web and the transformations of particulate and dissolved organic matter, such as size distribution and biochemical composition, as it descends through the water column. In order to underpin such models it is not enough to have estimates of the relative contributions of bacteria and zooplankton to total respiration in the mesopelagic zone – we also need to know the extent to which these two groups of organisms consume organic matter and alter its characteristics by repackaging and recycling it within the food web. Complex models will require intensive field programmes in order to constrain the many processes they incorporate. They are essential to future progress because it is only by understanding how not just the quantity, but also the quality of POC and DOC changes as material descends through the water column that a full picture of the dynamics of carbon cycling in the mesopelagic zone will become complete.

Table 1. Model parameters and default values (note, all parameters are dimensionless).

Parameter	Description	Value
ψ	partitioning of detritus to attached bacteria	0.76
α	solubilization losses: attached bacteria	0.50
ω_A	BGE: attached bacteria	0.24
ω_{FL}	BGE: free-living bacteria	0.15
ϕ_V	grazing losses to DOC: bacterivores	0.25
ϕ_H	grazing losses to DOC: detritivores	0.40
ϕ_Z	grazing losses to DOC: higher zooplankton	0.30
β_V	assimilation efficiency: bacterivores	0.72
β_H	assimilation efficiency: detritivores	0.60
β_Z	assimilation efficiency: higher zooplankton	0.66
k_V	NGE: bacterivores	0.44
k_H	NGE: detritivores	0.39
k_Z	NGE: higher zooplankton	0.39
ζ	particle microbial losses to detritivores	0.24

Figure Legends

Figure 1. Flow diagram of model. Detritus input from the euphotic zone (EZ) is cycled through the mesopelagic food web via POC (dark blue fluxes) and DOC (pink fluxes) and is ultimately respired as CO_2 (yellow fluxes); fluxes to small coloured circles enter either detritus, DOC or CO_2, according to colour code. The three main food web pathways are (1) via attached bacteria, (2) via detritivores and (3) via DOC and free-living bacteria (see text).

Figure 2. Model results for standard parameter settings (Table 1), normalized to detritus input from the euphotic zone (D_{EX}): detritus sources, DOC sources, detritus consumption (in the case of free-living bacteria via solubilization to DOC), production and respiration.

Figure 3. Model sensitivity to parameters: a) consumption of detritus, b) production, c) respiration. Parameters for zooplankton (detritivores, bacterivores, higher predators), ϕ, β and k, were varied simultaneously. Results are normalized to D_{EX}.

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