



Mesopelagic zone ecology and biogeochemistry – a synthesis

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ABSTRACT

The mesopelagic zone is the oceanic region through which carbon and other elements must pass in order to reach deeper waters or the sea floor. However, the food web interactions that occur in the mesopelagic zone are difficult to measure and so, despite their crucial importance to global elemental cycles, are not very well known. Recent developments in technology and new approaches have advanced the study of the variability in and controls upon the distribution and diversity of organisms in the mesopelagic zone, including the roles of respiration, recycling, and repackaging of particulate and dissolved organic material. However, there are remarkably few syntheses of the ecology and biogeochemistry of the microbes and metazoa that permanently reside or habitually visit this 'twilight zone'. Without this synthesis, it is difficult to assess the impact of ongoing changes in ocean hydrography and chemistry, due to increasing atmospheric carbon dioxide levels, on the biological carbon pump. This paper reviews what is known about the distribution of microbes and metazoa in the mesopelagic zone in relation to their activity and impact on global biogeochemical cycles. Thus, gaps in our knowledge are identified and suggestions made for priority research programmes that will improve our ability to predict the effects of climate change on carbon sequestration.

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1. Introduction

The mesopelagic or 'twilight' realm of the world's oceans is characterized by increased hydrostatic pressure, diminished light, high inorganic nutrient concentrations, and episodic food supply. Although operationally defined as the zone between 100–200 and 1000 m depth, it can also be defined in terms of key processes: the top of the mesopelagic as the base of the euphotic zone, where

light is too low for photosynthesis, and the bottom of the mesopelagic as the depth where downwelling irradiance is insufficient for vision to be effective in capturing prey. The mesopelagic is not a homogeneous layer, but encompasses strong gradients in environmental parameters, particularly at the interface with the euphotic zone and (when present) with oxygen minimum zones. These gradients influence the distribution and activity of the microbial and metazoan biota and elicit pronounced behavioral adaptations.

For the biogeochemist, the mesopelagic is the region where 90% of the organic carbon annually exported from surface waters is respired back to carbon dioxide. This respiration limits the

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extent of carbon sequestration from the atmosphere. Biogeochemical research has focused on understanding the observed pattern of particulate matter flux with depth (Martin et al., 1987; Buesseler et al., 2007), estimating the rates of microbial and zooplankton respiration (Dehairs et al., 1997; Arístegui et al., 2005; Steinberg et al., 2008a; Jacquet et al., 2008), and using models to describe the interactions between microbes, animals and material flux (Jackson and Burd, 2002; Stemann et al., 2004a; Anderson and Tang, 2010). For the zoologist, the mesopelagic contains a diverse community of animals that contribute to the repackaging and reprocessing of sinking and suspended organic material and is also the region where many animals retreat during the day to avoid predation by efficient visual predators. The mesopelagic thus provides a 'bedroom community' for these animals, as they move to the surface to feed at night and commute back downward at the end of the working 'day'. In the process, they contribute to vertical carbon flux by respiring carbon dioxide, releasing fecal pellets and dissolved organic matter below the euphotic zone, and falling victim to vertically structured carnivorous predators.

The mesopelagic is subject to both a continuous 'rain' and strong episodic inputs of organic matter from the euphotic zone. The complex mesopelagic food webs include animals that are omnivorous, change food preference as they grow, or switch between carnivory and particle feeding depending on the nature of the food supply (Robison, 1984). Within the mesopelagic biota, members of the same 'trophic' group can effect repeated transformation or repackaging of carbon, as evidenced by changes in the type of zooplankton fecal pellets and the Si:C ratio of sinking particles with depth (Carroll et al., 1998; Ragueneau et al., 2006; Wilson et al., 2008).

Understanding the mesopelagic zone is largely hampered by logistical constraints, causing knowledge of the diversity and function of the biota to be woefully inadequate. This is exemplified by the fact that current independent measures of microbial or zooplankton metabolic demands can each explain more than 100% of the particulate organic carbon (POC) flux attenuation within the mesopelagic (Steinberg et al., 2008a). In addition, there are still regular discoveries of new metazoan taxa (e.g., Matsumoto et al. 2003; Hopcroft and Robison, 2005), and recent genomic studies identified novel prokaryotic chemoautotrophic metabolic pathways in the oxygenated water column (Ingalls et al., 2006; Hamersley et al., 2007; Reinthaler et al., 2010). In a changing world, with warming, more acidic seas, and areal expansion of suboxic zones, we need an improved understanding of the ecological and biogeochemical interactions in the mesopelagic realm, one of the largest biomes on the planet, in order to predict the impact that environmental change may have on ecological diversity, elemental cycling and carbon sequestration.

This paper synthesizes current knowledge of the ecology and biogeochemistry of the mesopelagic zone, identifies gaps in our knowledge and prioritizes some areas for future research.

2. Microbial and metazoan ecology

The mesopelagic zone supports a highly diverse and active community of viruses, bacteria, archaea, protists, zooplankton and nekton (e.g., Koppelman and Frost, 2008; Arístegui et al., 2009; Fig. 1). The many physical and biogeochemical features of the mesopelagic zone help create specialized niches or 'hotspots' which enhance biological diversity, microbial growth and organic matter remineralization. These 'hotspots' include physical-chemical discontinuities such as water mass boundaries, currents, shear zones, internal tides and eddies, as well as the

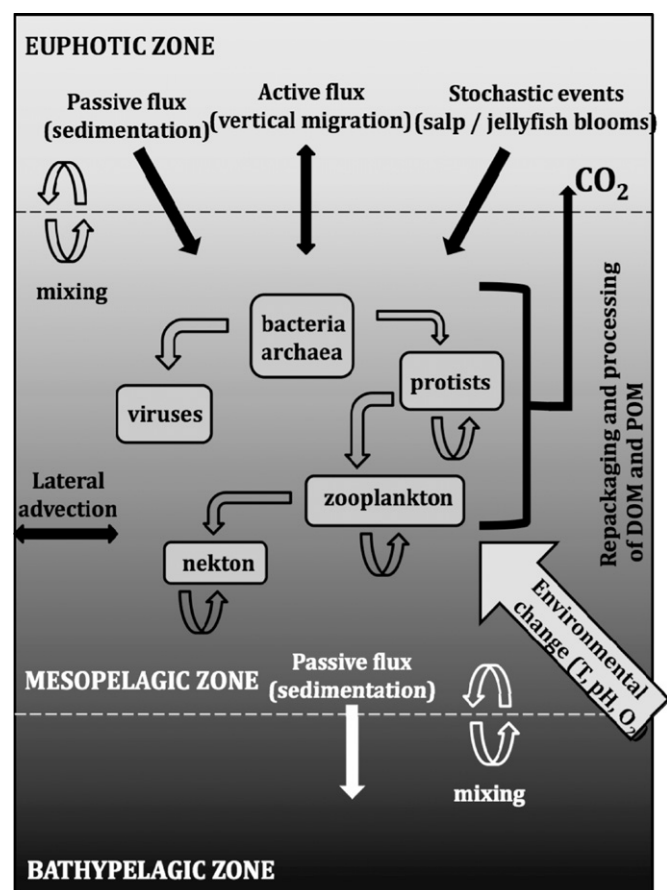


Fig. 1. Microbial and metazoan functional groups and interactions in the mesopelagic zone. Adapted from Koppelman and Frost (2008) and Arístegui et al. (2009).

microhabitats created by suspended and sinking particles, aggregates, colloids, gels and chemical plumes (Sameoto, 1986; Turley and Stutt, 2000; Kjørboe and Jackson, 2001; Pearre, 2003; Azam and Malfatti, 2007; Wishner et al., 2008).

2.1. Vertical distribution of functional groups

Several studies show prokaryotic, zooplankton and micronekton biomass declining exponentially with depth, from the euphotic to bathypelagic zones, by 2 to 4 orders of magnitude (Angel, 1989a; Yamaguchi et al., 2004; Reinthaler et al., 2006; Arístegui et al., 2009). However, microbial diversity has been shown in some cases to increase with depth (DeLong et al., 2006; Treusch et al., 2009). The abundance of gelatinous organisms and some radiolaria often increases with depth (Robison et al., 2010).

2.1.1. Viruses

Viral abundance in mesopelagic waters is of the order 10^{10} – 10^{12} viruses m^{-3} (Weinbauer et al., 2003; Magagnoli et al., 2007; Parada et al., 2007), and does not always decrease exponentially with depth; mesopelagic viral abundance maxima were seen in the Mediterranean and Baltic Seas (Weinbauer et al., 2003). The virus to prokaryote abundance ratio (VPR) does not decrease significantly with depth (Arístegui et al., 2009) except in the Central Atlantic, where Parada et al. (2007) found an increase in VPR from 9 at 100 m to 110 at 3500–5000 m. These very high VPRs suggest substantial allochthonous input of viruses from the

overlying water column via sedimenting particles (Parada et al., 2007).

2.1.2. Bacteria and archaea

Vertical stratification of the major free-living bacterial and archaeal groups, particularly between the euphotic and mesopelagic regions of the open ocean, is well documented (Gordon and Giovannoni, 1996; Giovannoni et al., 1996; Moeseneder et al., 2001; DeLong et al., 2006; Carlson et al., 2009; Fig. 2). While *Crenarchaeota* Group I comprise ~ 5% of total picoplankton in surface waters, they contribute up to 40% of picoplankton in the mesopelagic realm (Karner et al., 2001; Varela et al., 2008). Depth-specific distributions among ecotypes of specific bacterial lineages such as SAR11 have also been reported. For example, SAR11 ecotype II is the dominant contributor to the SAR 11 clade in the mesopelagic zone (Field et al., 1997; Morris et al., 2005; Carlson et al., 2009). Presumably, the observed vertical stratification of microbes is due, in part, to specialized microbial populations that can take advantage of vertical gradients in nutrients and energy availability. However, the specific roles of microbial taxa in the remineralization of organic matter of varying quality, the physiological mechanisms that enable them to utilize recalcitrant material, and factors that control their temporal dynamics within the mesopelagic zone remain elusive.

2.1.3. Protists

The diversity and community composition of the picoeukaryotes in the mesopelagic zone are poorly known, but a high number of as yet uncultured organisms are present, and only 10% of the picoeukaryotic taxa of the euphotic zone also occur in the mesopelagic (López-García et al., 2001; Lovejoy et al., 2006).

Based on cloning and sequencing studies, it is estimated that there are 700–800 protistan taxa in the global ocean, with the number of species in the deep ocean being 30–60% lower than that in the euphotic zone (Countway et al., 2007). This finding suggests that protistan species richness declines disproportionately more with depth than prokaryotic species richness does. Fukuda et al. (2007) measured abundance, cell size and biomass of nanoflagellates, and showed their significant role in the cycling of carbon in the mesopelagic subarctic Pacific. Nanoflagellate depth (100–1000 m) integrated biomass was $130 \pm 56 \text{ mg C m}^{-2}$, and the estimated nanoflagellate grazing could consume $70 \pm 46\%$ of the mesopelagic prokaryote production.

2.1.4. Zooplankton and nekton

The diel migration of zooplankton results in peaks in the abundance and biomass of many taxa at mesopelagic depths during the day (e.g., Angel, 1989b; Andersen et al., 2001; Steinberg et al., 2008b). For example, in the subarctic (Japanese time series site K2) and subtropical (Hawaii Ocean Time-series (HOT) station ALOHA) North Pacific, strong migrators such as ostracods peaked in the mesopelagic zone; they were nearly absent in the upper 50 m during the day, but were abundant in surface waters at night (Steinberg et al., 2008b). At northern latitudes, ontogenetic vertical migration of copepod species results in seasonal mesopelagic peaks in their abundance (Kobari et al., 2003; Bonnet et al., 2005). Conspicuous in the subarctic North Pacific is the ontogenetic migrating population of *Neocalanus* species copepods (Miller et al., 1984; Tsuda et al., 1999; Kobari et al., 2008). At site K2, ontogenetic migrating copepods on average comprised 62% of the mean mesozooplankton biomass between 150–1000 m, with different species of *Neocalanus* peaking at different mesopelagic depths (Kobari et al., 2008). Many micronekton taxa, such as myctophid fish, decapods, and medusae, also have abundance peaks in the mesopelagic zone (e.g., Angel and Baker 1982; Benoit-Bird and Au, 2006).

2.2. Factors affecting vertical distribution

2.2.1. Euphotic zone

The interface between the mesopelagic and the euphotic zone is highly heterogeneous, often characterised by layers of elevated concentrations of phytoplankton, bacteria and marine snow, which then influence zooplankton growth rates, fish larvae recruitment, and vertical flux of material into the mesopelagic. Sometimes substantially thinner than the 5-m scales routinely sampled with water bottles and nets, these discontinuity layers are difficult to sample for coincident measurements of physical, chemical and biological variables without disturbance. They also vary in depth spatially and temporally, due to processes such as internal waves, currents, episodic weather events and seasonal mixing, and so adaptive targeted sampling must be used, and new less intrusive sampling devices developed.

2.2.2. Water mass structure

The distribution of organisms in the meso- and bathypelagic ocean is not exclusively controlled by the vertical flux of organic carbon from the surface. Recent studies have shown the biogeographical distribution of the major groups of Bacteria and Archaea to be related to the temperature and salinity characteristics of distinct water masses (Teira et al., 2006). In addition, the ageing of deep water masses, as they follow the conveyor belt of thermohaline circulation, is accompanied by structural and functional changes in the prokaryotic community, likely reflecting changes in the quality and quantity of dissolved organic material (Teira et al., 2006).

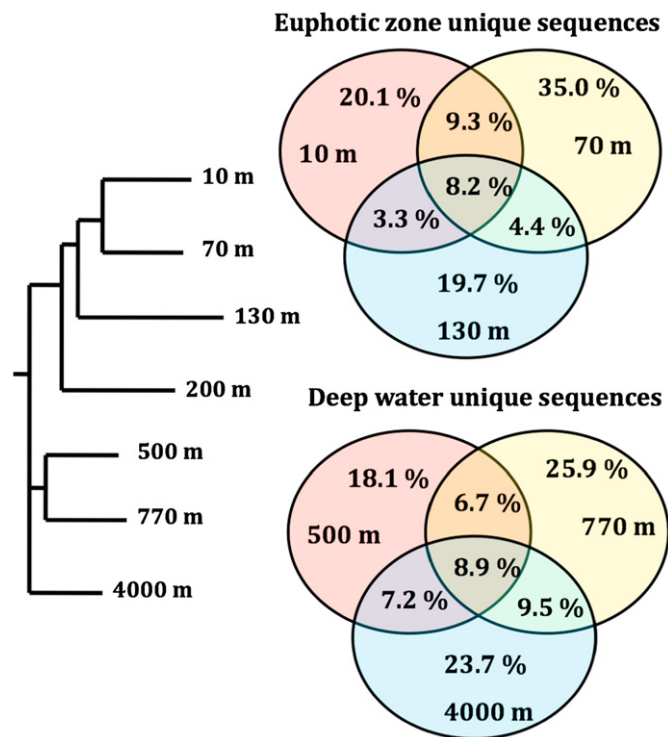


Fig. 2. Comparison of microbial gene sequences sampled from 6 depths at the Hawaii Ocean Time-series station ALOHA. The dendrogram shows a cluster analysis of sequence similarity or difference between all depths. The Venn diagrams show the percentage of sequences that were present only in euphotic zone sequences or only in deep water sequences, and the percentage of sequences which occurred in each subset of adjoining depths. Redrawn from DeLong et al. (2006).

2.2.3. Oxygen minimum zone

The mesopelagic zones in the eastern tropical Pacific Ocean and the tropical Indian Ocean contain depth layers with very low oxygen concentrations (less than $10 \mu\text{mol O}_2 \text{ kg}^{-1}$, or suboxic concentrations), while those in the tropical Atlantic Ocean encompass hypoxic layers (with oxygen concentrations less than 60 to $120 \mu\text{mol O}_2 \text{ kg}^{-1}$) (Stramma et al., 2008). These oxygen minimum zones (OMZs) support abundant and phylogenetically and metabolically very diverse microbial communities. OMZs play a vital role in the marine nitrogen cycle, allowing for the anaerobic conversion of fixed nitrogen into gaseous N_2 by prokaryotes at cell concentrations of 10^4 – 10^5 cells ml^{-1} (Kuypers et al., 2005; Ward et al., 2008). By contrast, oxygen is essential for the aerobic respiration of most metazoan fauna, and so many organisms are stressed or die under hypoxic conditions. The relative roles of microbes and zooplankton therefore may differ between aerobic and suboxic environments, as zooplankton abundance declines disproportionately more than that of bacteria (Anderson and Ryabchenko, in press). Mesopelagic copepod distribution and community structure can vary over short vertical distances across surprisingly small oxygen gradients at very low oxygen concentrations (Wishner et al., 2008). The vertical distribution of mesopelagic fishes is significantly affected by the presence of the OMZ in the Arabian Sea (Kinzer et al., 1993) and the Pacific Ocean (Matsui and Rosenblatt, 1987). Zones of enhanced biological and biogeochemical activity exist at the upper and lower boundaries of the OMZ (Wishner et al., 1995; Cornejo and Koppelman, 2006), while species from many taxa (including copepods, euphausiids, cnidaria, fish and squid) live entirely or part of the time (during diel or ontogenetic vertical migrations) within the most pronounced OMZs (Seibel and Drazen, 2007; Wishner et al., 2008). Animals living in these low oxygen environments have evolved remarkable physiological and morphological adaptations such as a small heart, enlarged gill surface, reduction in respiration rate, specialized respiratory proteins, and high lactate dehydrogenase enzyme activity (Childress et al., 1980; Johnson, 1982; Childress and Seibel, 1998; Herring, 2002).

2.2.4. Particle interactions

Deep-water prokaryotes exhibit distinct differences from their euphotic zone relatives, including a larger genome size, higher cell-specific respiratory activity, and a gene repertoire indicative of a predominantly surface-attached mode of life (Aristegui et al., 2005; DeLong et al., 2006; Reinthaler et al., 2006; Lauro et al., 2007; Gasol et al., 2008). This seems to indicate that deep-water prokaryotic activity is primarily associated with particles. However, attached-bacteria contribute only up to 30% of total bacterial biomass in mesopelagic waters (Cho and Azam, 1988; Turley et al., 1995; Ghiglione et al., 2007; Mével et al., 2008). Some phylogenetic analyses of particle-attached versus free living bacterial assemblages reveal distinct bacterial communities associated with the two types of environment (DeLong et al., 1993; Rath et al., 1998; Moeseneder et al., 2001), while other molecular fingerprinting studies support the 'generalist' hypothesis in which a large proportion of similar 'operational taxonomic units' are shared between both attached and free-living fractions (Hollibaugh et al., 2000; Moeseneder et al., 2001; Ghiglione et al., 2007).

Particle-associated bacteria assimilate the particulate material and solubilize the organic compounds as dissolved organic material (Fenchel, 2001, 2002; Kjørboe et al., 2002). Exoenzyme activity tends to be several times higher in attached than free-living bacteria (Becquevort et al., 1998), and bacteria colonizing particles produce amounts of ecto-hydrolases that would transform particulate organic material (POM) into dissolved organic material (DOM) at a rate faster than they can take it up (Cho and

Azam, 1988; Smith et al., 1992). This uncoupled solubilization and remineralization can result in significant release of dissolved compounds in the wake of a sinking particle, forming nutrient rich 'plumes' (Azam and Long, 2001; Kjørboe and Jackson, 2001). Free-living bacteria in the deep-ocean may sense the enriched nutrient environment around a particle and actively swim towards it (Jackson, 1989; Blackburn and Fenchel, 1999; Kjørboe and Jackson, 2001), forming a 'detritosphere' ecosystem around the particle (Biddanda and Pomeroy, 1988).

While a number of studies have focused on prokaryote particle association, considerably less is known about associations between particles and higher trophic levels (protists and metazoa) in the mesopelagic zone (Caron, 1987; Lawrence and Snyder, 1998; Artolozaga et al., 2002; Kjørboe, 2003; Kjørboe et al., 2004; Lampitt et al., 2009). Silver et al. (1984) found high concentrations of ciliated protists on sinking marine snow particles down to bathypelagic depths in the NE Pacific Ocean. The ciliate taxa found on deep-water particles were endemic to populations below the euphotic zone, and not simply 'riding' sinking particles from surface waters.

The discarded mucous 'houses' of giant larvaceans provide a habitat and a food source for a variety of mesopelagic microbes (Silver et al., 1998) and mesozooplankton (Steinberg et al., 1994). Up to an order of magnitude more zooplankton were found on houses compared to the same volume of surrounding seawater, and many of the zooplankton taxa possessed 'benthic-like' morphology and feeding strategies, such as *Oncaea* spp. copepods, polychaetes, and amphipods (Steinberg et al., 1994). Particle-associated zooplankton also contribute to remineralization of POC at depth. Measurement of community respiration on giant larvacean houses indicated that approximately 1–8% of house carbon is used daily to sustain community respiration, and a mean of 6% and up to 43% of house carbon is ingested by zooplankton each day (Steinberg et al., 1997). In addition to particles and aggregates, the bodies of resident animals provide a means of attachment, shelter and food for other organisms. For example, the tunicate *Doliolula equus* provides substrate for symbionts which include a mutualist hydroid, commensal ciliates (themselves hosts to bacteria and flagellates) and a parasitic amphipod (Robison et al., 2005a).

The quantity and quality of particles, together with subtle metazoan feeding specializations, may be important determinants of mesopelagic community structure. Wishner et al. (2008) documented feeding specialization between two co-occurring omnivorous copepods feeding on different kinds of particles. Steinberg et al. (2008b) found mesopelagic peaks in a number of taxa known to feed on suspended or sinking detritus, including calanoid and poecilostomatoid (e.g. *Oncaea* spp.) copepods, salps, polychaetes, phaeodarian radiolaria, harpacticoid copepods and ostracods.

2.3. Temporal variability

The physical, chemical and biological interactions occurring in the mesopelagic layer operate on a range of time and space scales from seconds to decades and from microns to tens of kilometers (Fig. 3). Time-series programs provide the ideal opportunity to resolve seasonal, inter-annual and decadal variability of mesopelagic community structure in the context of other relevant biogeochemical data. However, episodic events and processes occurring at time scales shorter than 1 month require more targeted sampling strategies.

2.3.1. Bacteria

At ALOHA, Karner et al. (2001) demonstrated over a two year period that *Crenarchaeota* vary temporally within the mesopelagic.

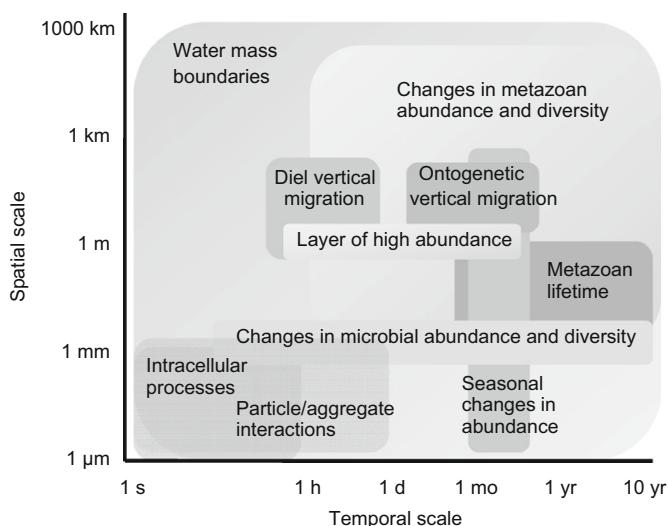


Fig. 3. Spatiotemporal representation of the interactions between physico-chemical and ecological processes occurring in the mesopelagic zone. Note the spatial scale on the y-axis encompasses vertical (depth) and horizontal (areal) scales, depending on the process.

Seasonality of several bacterioplankton lineages has also been shown within the upper mesopelagic zone at the Bermuda Atlantic Time-series Study (BATS) site, linked to the deep mixing event that occurs there. Every winter/spring the deep mixed layer extends into the mesopelagic zone entraining nutrients from depth into the euphotic zone (Steinberg et al., 2000) and exporting suspended organic matter into the mesopelagic zone (Hansell and Carlson, 2001; Goldberg et al., 2009). The time lag between mixing and increased prokaryotic abundance (Morris et al., 2005) suggests that the upper mesopelagic populations are responding to organic and/or inorganic substrates introduced during convective overturn. Terminal restriction fragment length polymorphism (T-RFLP) patterns generated from a decade of DNA collected from the surface and upper mesopelagic zone at BATS (140–300 m) reveal a marked shift in the bacterioplankton community structure following convective overturn. Specialized communities of the clades SAR11 (subcluster II), marine *Actinobacteria*, SAR202 and OCS116 increase in their relative contribution to the total mesopelagic community following convective mixing (Morris et al., 2005; Carlson et al., 2009; Treusch et al., 2009). These data suggest that specialized communities are capable of responding to and remineralizing the surface derived and seemingly recalcitrant DOM that was introduced during mixing. Goldberg et al. (2009) demonstrated that exported DOM became diagenetically altered through time within the mesopelagic zone; however, direct links between the spring mesopelagic bloom populations and the remineralization of polymeric/recalcitrant organic matter remains to be established.

2.3.2. Protists

Tanaka and Rassoulzadegan (2002, 2004) measured abundances of heterotrophic prokaryotes, heterotrophic nanoflagellates, and ciliates from 5 to 2000 m every month from May 1999 to March 2000 at the DYnamique des Flux de mAtière en MEDiterranée (DYFAMED) time-series station in the NW Mediterranean Sea. All three groups varied seasonally within the upper 1000 m. Gowing et al. (2003) showed seasonal variability in mesopelagic microplankton biomass in the Arabian Sea, related to surface productivity and increased mesopelagic organic carbon flux.

2.3.3. Zooplankton and nekton

The strength of the seasonal change in mesopelagic metazoa appears to vary with region, depending on the processes in the

overlying water column. Wishner et al. (1998) detected weak seasonal trends in mesozooplankton biomass in the mesopelagic zone of the Arabian Sea. Life history changes in the copepod species (*Lucicutia grandis*) living at the lower oxycline (about 600–900 m) suggested a response to the seasonal input of POC from monsoon-driven surface production. Higher abundances of young stages of this species occurred shortly after seasonal monsoon flux events recorded in sediment traps (Wishner et al., 2000). Tseitlin and Rudyakov (1999) found higher mesopelagic zooplankton biomass in the summer SW monsoon period compared to the winter NE monsoon period in the northern Indian Ocean, while Koppelman and Weikert (1999) measured four-fold higher mesopelagic mesozooplankton abundance in spring than in summer in the NE Atlantic. Strong seasonality, linked to regional upwelling in Monterey Bay, has been shown for two groups of mesopelagic siphonophores that feed on krill and copepods (Robison et al., 1998; Silguero and Robison, 2000; Fig. 4).

In addition to seasonal variability, decadal-scale changes in mesopelagic zooplankton have been documented. Migrant zooplankton biomass at ALOHA has increased significantly over the past 12 years (Hannides et al., 2009). This has increased the importance of phosphate removal via zooplankton excretion at depth relative to sinking fluxes, suggesting that active transport may be a major driving force for enhanced phosphate limitation of primary production in the North Pacific Subtropical Gyre (Hannides et al., 2009). Over the same time period, migrant zooplankton biomass has also increased at the BATS site in the North Atlantic subtropical gyre, doubling the active transport of carbon to the mesopelagic zone (Steinberg et al., 2008c).

2.4. Regional comparisons

Only a limited number of studies compare and contrast mesopelagic microbial and metazoan distribution, diversity and activity between ocean basins, water masses or biogeochemical provinces (Teira et al., 2006; Steinberg et al., 2008b; Aristegui et al., 2009). Agogue et al. (2008) investigated the prevalence of archaeal genes coding for the major enzyme involved in ammonia oxidation in samples along a latitudinal transect in the North Atlantic Ocean. The results indicate that the proportion of *Crenarchaeota* which oxidize ammonia decreases markedly from subpolar to equatorial regions. Basin scale geographic variability in mesopelagic bacterial biomass and production in the Pacific Ocean has been shown to be related to differences in organic carbon supply (Nagata et al., 2000, 2001), while latitudinal changes in the relative contribution of *Crenarchaeota* Group I to total mesopelagic picoplankton abundance in the eastern N Atlantic may be due to succession and ageing of deep water masses (Varela et al., 2008).

Overall, the abundance of prokaryotes (P) and heterotrophic nanoflagellates (HNF) in the mesopelagic zone are closely related. However, there are unexplained regional differences in the ratio of P/HNF. Aristegui et al. (2009), using a global dataset, found that the average P/HNF ratio remains almost constant from the surface to the bathypelagic in the Pacific and Atlantic Oceans, whereas in the Mediterranean Sea the ratio increased with depth. These differences were due to a much lower abundance and a sharper decrease with depth of HNF in the Mediterranean Sea, compared to the other oceanic regions. This lower HNF abundance in the Mediterranean Sea could be due to a higher abundance of ciliates (Tanaka and Rassoulzadegan, 2002).

Latitudinal studies of plankton biomass in the N. Pacific Ocean indicate an order of magnitude decrease in integrated mesopelagic zooplankton biomass from the subarctic to the subtropics (Yamaguchi et al. 2004; Steinberg et al. 2008b). Higher primary

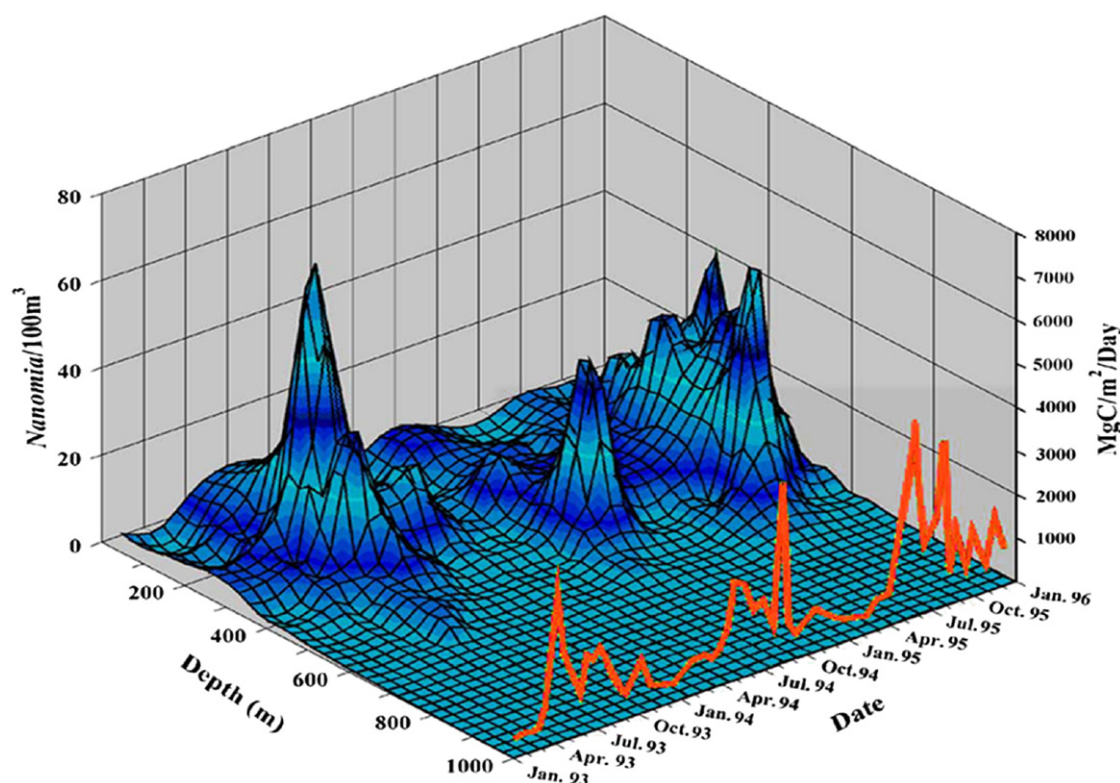


Fig. 4. Abundance and depth distribution of the mesopelagic siphonophore *Nanomia bijuga* in Monterey Bay, USA. Black line is euphotic zone primary productivity in $\text{mg C m}^{-2} \text{d}^{-1}$. Redrawn from Robison et al. (1998).

production in surface waters in the subarctic compared to the subtropical latitudes is thus fueling higher secondary production at depth. Regional comparison of mesopelagic mesozooplankton taxonomic structure in the subarctic and subtropical N. Pacific Ocean indicates that a higher proportion of the biomass in the subarctic occurs within the larger ($> 2 \text{ mm}$) size classes, due to the abundance of large calanoid copepods (*Neocalanus* spp., and *Eucalanus bungii*) (Steinberg et al., 2008b). Koppelman and Frost (2008) found significant differences between mesozooplankton distribution and activity in the N. Atlantic Ocean, and the Mediterranean and Arabian Seas.

The considerable variability within the life cycles of mesopelagic animals allows them to adapt to regional differences in their habitat. For example, populations of the mesopelagic fish *Vincegueria nimbaria* show variability in egg size and fecundity, depending on whether they occur in high- or low-productivity regions (Herring, 2002). Doliolids, which typically alternate sexual with asexual reproductive phases, can shift to a repeating single mode when environmental conditions dictate that one is likely to be more successful than the other (Robison et al., 2005a). Similar adjustments can be seen when low oxygen, changes in competition for food, or regional productivity affect a part of a species' range. Differences in productivity or hydrographic conditions may also affect energy content and composition of mesopelagic fauna. A comparison of chemical composition of Antarctic mesopelagic fishes with similar species from tropical, subtropical and temperate systems indicated differences (e.g. protein content) for some genera such as *Electrona* and *Cyclothone*, but there were no latitudinal trends in other genera such as *Bathylagus* (Donnelly et al., 1990).

A regional comparison of mesopelagic macrozooplankton communities, with an emphasis on fragile gelatinous taxa, was recently undertaken using an underwater video profiler (UVP, Stemmann et al. 2008). The distribution of gelatinous and other taxa from 0–1000 m were compared in nine regions of six oceanic

basins. Macrozooplankton composition was significantly different between all regions except adjacent regions of the North Atlantic. The authors suggest that mesopelagic communities are structured on large, basin scales, but possibly not on smaller, frontal scales. The main difference between regions was a decrease in the proportion of all gelatinous carnivores and chaetognaths from 95% in high latitude regions, to 15% in low latitudes.

3. Behaviour and sensory communication

The ecology and biogeochemistry of microbes and metazoa in the mesopelagic are influenced by behavioural traits such as motility, migration and sensory communication. The separation in depth of feeding and excretion by vertically migrating mesozooplankton is an obvious example of a behavior that has a profound influence on the vertical flux of carbon and associated elements. The characteristic physical environment of the mesopelagic (high pressure, reduced turbulence and low light) selects for body forms, and feeding and communication mechanisms that would be impractical at shallower depths (Robison, 2004; Koppelman and Frost, 2008).

A large fraction of free-living bacteria are motile, and can sense the gradients or plumes of organic matter and nutrients surrounding particles or aggregates and actively swim towards them (Kjørboe and Jackson, 2001). Bacterial isolates from marine aggregates also display antagonistic activities towards other bacteria, which may inhibit their development and so influence the community structure around particles (Martínez et al., 1996; Grossart et al., 2003; Aristegui et al., 2009). Male copepods track their mates by following pheromone trails produced by females (Yen et al., 1998; Kjørboe and Bagøien, 2005).

The sensory capabilities of mesopelagic metazoans have largely been inferred from the sensory structures themselves, because direct behavioral observations are rare. Vision, even in the dim

illumination of the lower mesopelagic, is clearly important to many micronektonic fishes and squids, which have expended considerable evolutionary energy to develop extraordinarily capable eyes. Among their visual adaptations are heightened sensitivity, binocular vision, and the ability to distinguish between protective counter illumination and downwelling daylight (Warrant and Locket, 2004; Robison and Reisenbichler, 2008). Sensitivity to light is also critical for triggering their diel vertical migrations (Frank and Widder, 2002), with different species often tracking particular isolumines. Recent work highlighted a lunar cycle that affects migration depth and scattering layer density that may create a monthly periodicity in planktonic communities and carbon flux (Hernández-León et al., 2002; Benoit-Bird et al., 2009). For example, vertically migrating planktivorous fish remained in deep water during the full moon period near the Canary Islands. Reduced predation by these fish resulted in increased euphotic zone mesozooplankton abundance. During the dark lunar phase (new moon), these fish moved into surface waters and mesozooplankton abundance decreased (Hernández-León et al., 2001). Phases of the lunar cycle may therefore result in changes in the structure of planktonic communities, and changes in carbon flux to depth. Lunar modification of active transport of carbon by diel vertical migrators could help explain periodicity in the passive sinking flux and the mismatch between flux and respiration budgets (Steinberg et al., 2008a).

Coupled to the capacity for perceiving even a few photons of light, is the ability to produce it. Bioluminescence seems to be the most widespread form of communication in the deep sea with the vast majority of deep-living inhabitants capable of producing their own light (Herring, 2002). Bioluminescence is used to locate food, lure prey, attract mates, and remain camouflaged from or deter predators. Functional crossover between the microbial biota and the metazoan fauna occurs with the symbiotic incorporation of luminous bacteria into the light organs of certain fishes (Herring, 2002).

Unlike the micronekton and most crustacean zooplankton, gelatinous mesopelagic animals such as medusae, ctenophores, and siphonophores typically lack eyes. Nevertheless, they are just as likely to be bioluminescent. In most cases light production is triggered by mechanical stimulation and its functional role is believed to be that of a 'burglar alarm' to drive off potential predators (Widder, 1999). Some siphonophores are known to use their luminescence to attract prey (Haddock et al., 2005), and this function seems likely for other gelatinous predators as well.

Sensory capabilities for environmental signals other than light are not well known for most mesopelagic animals. Chemoreception enables the hydromedusa *Mitrocoma cellularia* to sense prey (Tamburri et al., 2000), and the behavior of many gelatinous predators suggests that this capability is widespread. A number of fishes have large nasal rosettes and expanded olfactory lobes in their brains (Marshall, 1971), presumably for finding food they cannot see. It also seems likely that aposematic chemical signals are used to warn potential predators away from the toxic compounds that protect soft-bodied mesopelagic species. Little is known about the use of sound by mesopelagic animals but many seem to be sensitive to low-frequency vibrations, detected by sensory filaments such as the lateral line organs of fishes (Marshall, 1971). Related sensory systems in sharks can detect the electric fields generated by the presence of other animals (Kalmijn, 1982), but these capabilities have yet to be demonstrated for any mesopelagic species.

4. Microbial and metazoan function

Microbial and metazoan processes are responsible for the significant amount of organic matter transformation, solubilization and remineralization which occurs within the mesopelagic zone.

4.1. Biological pump

Mesopelagic microbes and metazoa play key roles in the mechanisms involved in the 'biological pump' i.e. the reprocessing and downward advection of dissolved organic matter, the sinking flux of particulate matter, and the active transport of organic matter and associated biominerals via vertical migration.

DOM and POM range over a size continuum ($< 10^{-4}$ to $> 10^0$ m) that includes colloids, gels, suspended and sinking particles, and larger sinking aggregates. DOM and POM change systematically with depth, becoming more diagenetically altered as depth increases (Skoog and Benner, 1997; Lee et al., 2000; Goldberg et al., 2009). The bulk DOM pool represents a continuum of biological lability, from refractory material turning over on time scales of centuries to millennia to very labile material turning over on time scales of minutes to days. The portion of the dissolved organic carbon (DOC) pool resistant to rapid microbial degradation, turning over on time scales of months to years, is termed the 'semi-labile' DOC pool (Kirchman et al., 1993; Carlson and Ducklow, 1995). This semi-labile fraction enters the deep ocean via convective overturn (Carlson et al., 1994; Hansell and Carlson, 2001), isopycnal exchange (Hansell et al., 2002) or in situ production (Ogawa et al., 2001). With increasing depth, the bulk DOM is successively depleted in phosphorus (DOP) and nitrogen (DON), leading to an overall increase in the DOC:DON:DOP ratio (Benner, 2002). The lower reactivity of deep water DOM is reflected in low prokaryotic growth yields (Reinthal et al., 2006) and expression of more extracellular enzymes on a per-cell basis (Baltar et al., 2009).

Gravitational sinking rates of particles, which originate mainly from phytoplankton and zooplankton activity in the euphotic zone, vary from $< 1 \text{ m d}^{-1}$ for small particles to $> 1000 \text{ m d}^{-1}$ for large aggregates. Mesopelagic organisms modify this sinking flux by both repackaging organic carbon into faster-sinking particles such as fecal pellets (e.g., Wilson et al., 2008; Fig. 5) and fragmenting larger aggregates into smaller slower-sinking particles (De La Rocha and Passow, 2007; Anderson and Tang, 2010).

The biotic processing or repackaging of POC is linked to the recycling of biominerals such as opal and calcium carbonate. Mesopelagic fish contribute to organic and inorganic carbon cycling through their slow release of dissolved organic compounds (Robison and Bailey, 1981) and production of precipitated carbonates that are defecated and transported downward (Wilson et al., 2009). The biotic fragmentation or repackaging of diatom aggregates influences the balance between the recycling of biogenic silica and its sedimentation (Moriceau et al., 2007a). Moriceau et al. (2007b) used a simple advection-reaction model with two pools of biogenic silica – free diatom cells and large aggregates – to confirm that the depth of biogenic silica recycling is influenced more by particle formation than by dissolution rates or the ballast effect of the diatom frustules. In a review of organic carbon to biogenic silica ratios, Ragueneau et al. (2006) highlighted the dynamic response of the mesopelagic foodweb to the elemental composition of the particles sinking from the euphotic zone into the mesopelagic; provinces (e.g., Equatorial Pacific) with a large difference between the remineralization rates of silicate and carbon in the euphotic zone had a small difference in the silicate and carbon remineralization rates in the mesopelagic. Conversely, regions (e.g., Southern Antarctic Circumpolar Current) with low decoupling between the Si and C cycles in the euphotic zone had large differences in silicate and carbon remineralization rates in the mesopelagic (Fig. 6).

The diel vertical migration of zooplankton and micronekton is an important component of the 'biological pump'. By feeding in surface waters at night, and metabolizing (i.e. respiring, excreting, and egesting) surface-ingested POM at mesopelagic depths during

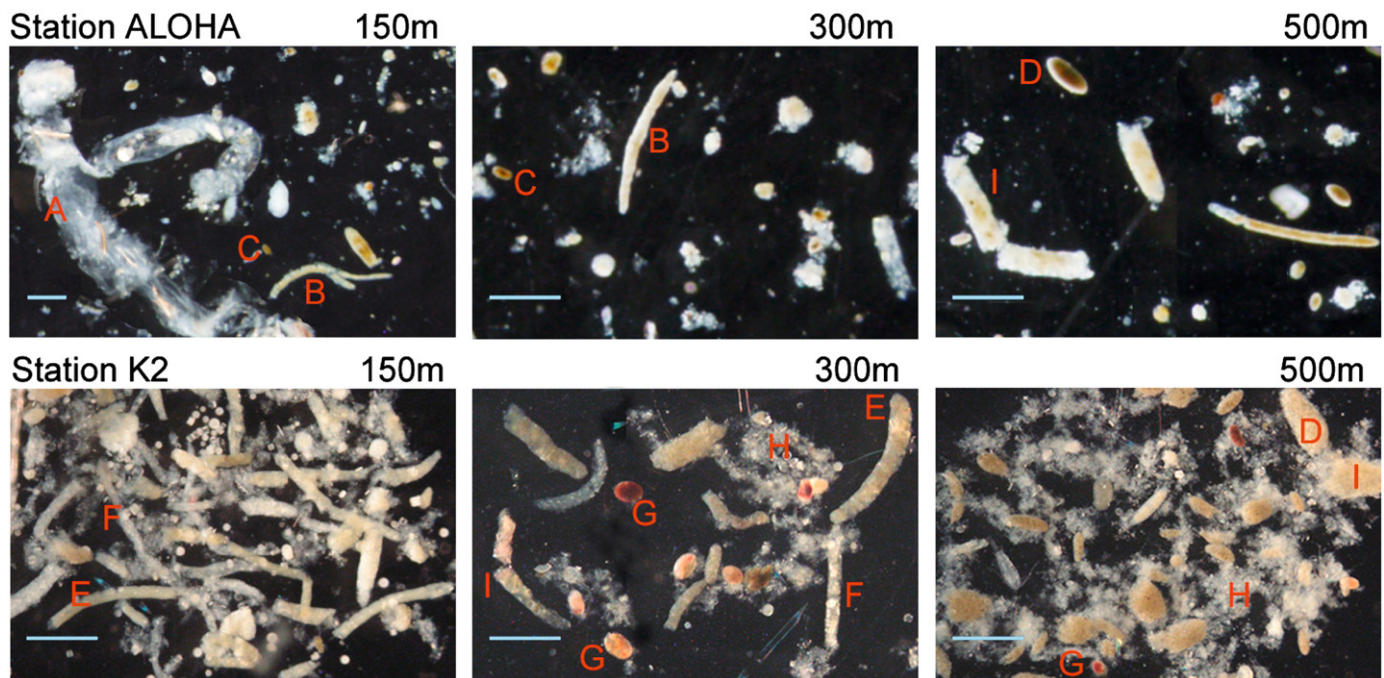


Fig. 5. Changes in zooplankton fecal pellets with depth indicating repackaging in the mesopelagic zone. Major types of pellets identified from sediment trap samples at the Hawaii Ocean Time-series (HOT) station ALOHA in the subtropical Pacific, and Japanese time-series station K2 in the subarctic Pacific. Scale bar is 500 μm . (A) heteropod *Carinaria* spp. (B) large copepod or euphausiid, (C) small copepod, (D) larvacean, (E) *Neocalanus* spp., (F) Euphausiid, (G) unknown carnivorous zooplankton, (H) fecal 'fluff,' (I) broken pellet. From Wilson et al. (2008).

the day, migrators 'actively transport' carbon, nitrogen, and phosphorus to depth (e.g., Longhurst et al., 1990; Steinberg et al., 2002; Hannides et al., 2009). For carbon, this active transport may be on average 15–20% of the gravitational flux of POC, but during seasons of high primary production or in environments with high zooplankton biomass, active transport is comparable to or exceeds POC transport by sinking particles (Zhang and Dam, 1997; Le Borgne and Rodier, 1997; Steinberg et al., 2000; Al-Mutairi and Landry, 2001; Hannides et al., 2009). Additional processes that increase the active flux are daytime mortality of diel migrators at depth (Zhang and Dam, 1997; Al-Mutairi and Landry, 2001) and ontogenetic (seasonal) migration (Kobari et al., 2008).

4.2. Respiration and remineralisation

Approximately 90% of the organic carbon exported from the surface ocean is respired within the mesopelagic zone, producing about 30% of the total biological CO_2 production in the oceans (del Giorgio and Duarte, 2002; Arístegui et al., 2005). Average depth integrated (150–1000 m) microbial respiration rates are of the order $3\text{--}4 \text{ mol C m}^{-2} \text{ a}^{-1}$, or $1.2 \text{ Pmol C a}^{-1}$ (Arístegui et al., 2005), while mesopelagic zooplankton respiration is estimated to be $0.18 \text{ Pmol C a}^{-1}$ (Hernández-León and Ikeda, 2005). Up to 80% of the variability in a global dataset of epipelagic, mesopelagic and bathypelagic copepod respiration could be explained by body mass, temperature, oxygen saturation and depth of occurrence (Ikeda et al., 2007). Weight-specific respiration rates of zooplankton and fish do not necessarily decrease with depth (when corrected for temperature), but rather are associated with lifestyle. The 'visual interactions hypothesis' explains why non-visual feeders (copepods, gelatinous animals) show similar weight-specific metabolic rates as their shallow water relatives, while active visual predators such as fish may show decreased weight-specific rates with depth (Seibel and Drazen, 2007).

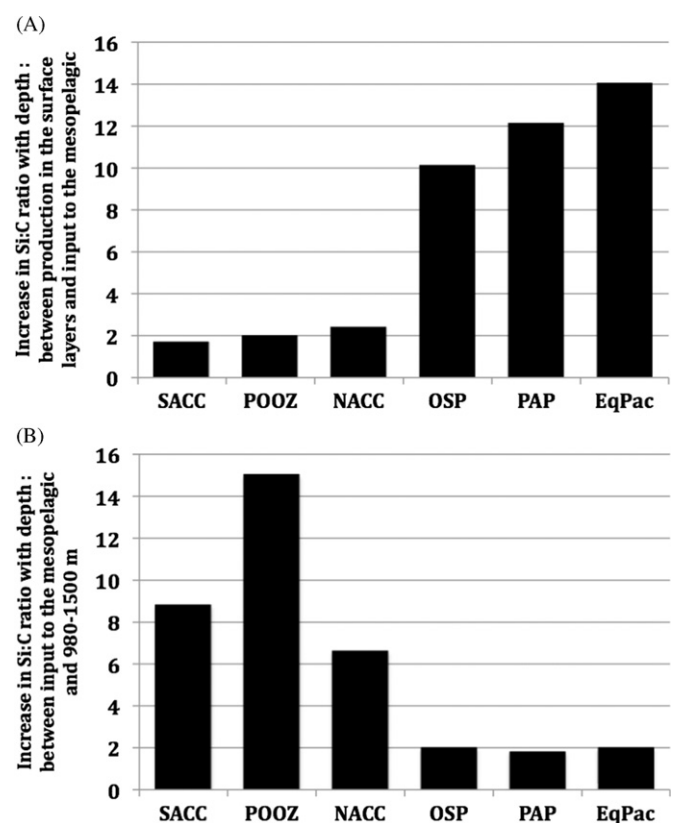


Fig. 6. Increase in particulate molar Si:C ratios between (A) production and input to the mesopelagic zone and (B) input to the mesopelagic zone and collection at 980–1500 m at stations SACC (Southern Antarctic Circumpolar Current, Pacific sector of the Southern Ocean), POOZ (Permanently Open Ocean Zone, Indian Ocean sector of the Southern Ocean), NACC (Northern Antarctic Circumpolar Current, Pacific sector of the Southern Ocean), OSP (Ocean Station Papa), PAP (Porcupine Abyssal Plain), and EqPac (Equatorial Pacific). Adapted from Ragueneau et al. (2006).

Regional estimates of the vertical inputs of carbon to the mesopelagic zone tend to be much lower than those required to support the magnitude of measured microbial respiration (e.g. Reinthaler et al., 2006; Baltar et al., 2009). This mismatch between geochemical estimates and ecological rate measurements may be due to an underestimation of lateral transport of organic carbon or to a lack of information on organisms which occur as massive episodic blooms but are extremely difficult to sample, e.g., gelatinous animals (Herndl et al., 2008). Rationalization of this mismatch is investigated in detail by Burd et al. (2010).

4.3. Chemoautotrophy

Recent data suggest that prokaryotic chemoautotrophy in the deep oxygenated water column might be far more important than previously assumed (Herndl et al., 2005; Ingalls et al., 2006; Reinthaler et al., 2010). Archaeal ammonia oxidation uses inorganic carbon as the carbon source, and therefore represents a major source of newly synthesized organic carbon for use by the entire foodweb. Prokaryotic carbon fixation in the meso- and bathypelagic zones of the North Atlantic is within the same order of magnitude as heterotrophic microbial activity, amounting to 1–2.5 mmol C m⁻² d⁻¹ or 15–53% of the phytoplankton export production (Herndl et al., 2005, 2008; Reinthaler et al., 2010).

5. Sensitivity to global change

Our understanding of the impact of global change on microbial and metazoan community structure, abundance, distribution and phenology relies crucially on decadal time-series studies – either at eulerian stations or on regular transects of ships of opportunity (Hays et al., 2005). Several examples of long-term change in plankton abundance have been attributed to the interacting effects of climate change, eutrophication, and overfishing (e.g., Lynam et al., 2004).

5.1. Increasing temperature

As a consequence of global warming, by 2100, ecosystems will be exposed to temperatures that will be among the highest experienced in the past 740,000 years (Solomon et al., 2007). Since metabolic rate increases with temperature with a Q₁₀ of 2–4 (White et al., 1991), increasing seawater temperatures may have a direct effect on the degradation of organic matter (López-Urrutia et al., 2006; López-Urrutia and Morán, 2007).

Predicting the impact of increasing temperature on the mesopelagic ecosystem is complicated, as temperature acts at a range of levels – including a) direct physical-chemical effects such as changing dissolved gas concentration and chemical speciation, and changing dissolution rates of mineral ballast, b) direct effects on metabolic rates and physiology, c) indirect oceanographic effects such as changing ocean circulation, stratification, viscosity, and upwelling thereby changing the chemical environment and nutrient supply and hence organism growth and production, and d) differential effects on different species or trophic groups thereby affecting predator/prey or competitive interactions between species. Increasing sea surface temperatures have had measureable effects on the timing of the peak abundance of euphotic zone plankton, causing a mismatch in synchronization between meroplankton and their prey (Edwards and Richardson, 2004). This disruption of synchrony between trophic levels could therefore have severe implications for energy flow to higher trophic levels such as fish, and export of organic carbon to the mesopelagic.

5.2. Expansion of oxygen minimum zones

The OMZs in the central and eastern tropical Atlantic and equatorial Pacific Oceans have expanded and intensified during the past 50 years (Stramma et al., 2008). This observation supports model predictions of a loss of about 25% of the current oxygen content of the global ocean by the end of the century due to changes in circulation patterns, warming and increased stratification (Bopp et al., 2002). Increasing areas of suboxia will lead to increased prokaryotic chemoautotrophy, and therefore have a significant impact on nitrogen and carbon cycling. Changes in the extent of OMZs may also affect zooplankton distributions and abundances, especially with respect to vertical migrators. A mismatch between the demand for oxygen and the capacity for oxygen supply to tissues is the first mechanism to restrict animal tolerance to thermal extremes (Pörtner and Knust, 2007). With increasing temperatures, the aerobic euphotic zone will be reduced, limiting the habitat for some commercial fishery species, while some plankton and vertical migrators adapted to suboxic conditions, may expand their ranges. Since total zooplankton biomass is smaller by several orders of magnitude in OMZs compared to oxygenated water columns (Wishner et al., 1998), the expansion of this habitat would likely result in a reduction in mesopelagic zooplankton biomass and a consequent reduction in zooplanktonic repackaging of sinking material in the mesopelagic zone. Billet et al. (2006) suggested that the mass deposition of the scyphozoan jellyfish *Crambionella orsini* observed in the deep Arabian Sea could be due to the reduction in degradation rate of jellyfish carcasses as they passed through the intense OMZ above.

5.3. Increasing carbon dioxide, decreasing pH

Over the last 250 years the oceans have taken up nearly a third of the anthropogenic carbon dioxide (CO₂) released into the atmosphere by the burning of fossil fuels (Sabine et al., 2004). This increase in ocean absorption of CO₂ leads to a reduction in pH and changes in the carbonate chemistry of the ocean, referred to as ocean acidification (Doney et al., 2009). Laboratory studies of the response of planktonic organisms such as coccolithophorids to increases in CO₂ are ambiguous, with results including reductions, no change, and increases in calcification in response to increases in CO₂ (reviewed in Fabry, 2008; Doney et al., 2009). Shell dissolution in planktonic foraminifera occurs in response to decreases in pH (Orr et al., 2005; Fabry et al., 2008), but the effects of increasing CO₂ and decreasing pH on mesopelagic fauna is virtually unknown.

Increasing the acidity of seawater can lead to hypercapnia in body fluids and tissues, which affects the ability of blood to carry oxygen and imposes other physiological stresses, including a reduction in protein synthesis, which is necessary for reproduction and growth (Seibel and Walsh, 2001). For example, under conditions where its blood pH declines by 0.2 pH units, the mesopelagic mysid *Gnathopausia ingens* would experience a reduction of 50% in the bound oxygen level of its blood (Childress and Seibel, 1998).

5.4. Over-fishing

Mesopelagic fishes, squids, and krill are principal food items for many of the most heavily harvested commercial species. The removal of top predators from the oceanic food chain can have profound effects on pelagic ecosystems (Frank et al., 2005; Worm et al., 2005, 2006). If a harvested species is pushed to commercial extinction, it may not recover when fishing stops. In some cases it

may be replaced by another species that fills its niche and prevents its recovery (Robinson, in press). Species with high fecundity and short generation times, such as jellyfish and squids, are particularly suited to the opportunistic replacement of tunas and other large, pelagic fishes that mature slowly (Lynam et al., 2006). Replacement species may not feed on the same proportions of prey types as the species they follow, producing an altered predation pressure on the mesopelagic community, affecting its diversity, and structure. One example of the impact of over-fishing, may be the invasion into temperate waters off California and Chile of the Humboldt squid, *Dosidicus gigas* (Zeidberg and Robison, 2007). This large predator may have expanded its range because commercial fishing and the depletion of tuna in tropical waters led to rapid population growth of the squid, when competition from and predation by the tuna was removed. Consequences of this invasion into temperate waters included reductions in commercial populations of hake, as well as differential impacts on many mesopelagic species (Field et al., 2007; Alarcón-Muñoz et al., 2008). Commercial fishing pressure can also impact mesopelagic species through the process of 'fishing down the food web' (Pauly et al., 1998). As the populations of top predators have declined, fishing effort has shifted to species at lower trophic levels. In some cases mesopelagic fishes (Valinassab et al., 2007) and krill (Jones and Ramm, 2004) have themselves become the targets for commercial fisheries.

6. Development of techniques

The study of the mesopelagic zone is severely limited by our usual sampling methods. The vast size of the ocean, small vertical-scale heterogeneity, short temporal-scale research ship activities, intense hydrostatic pressure, and the avoidance tactics of metazoa all contribute to the lack of representativeness of net, trap and bottle samples. A more representative sampling strategy depends on the development of autonomous and remotely operated instrumentation, molecular and environmental sensors for deployment on long-term moorings, sampling and incubation vessels that maintain ambient pressure, and use of laboratory manipulations which mimic anticipated changes in the nutrient and substrate environment encountered by mesopelagic organisms.

For example, the use of remotely operated vehicles (ROVs) has revolutionized our appreciation of the complexity and heterogeneity of metazoan diversity in the mesopelagic (Steinberg et al., 1994; Robison et al., 1998; Robison, 2004; Haddock et al., 2005), and made it possible to recognize the importance of large particles, not typically sampled by sediment traps, to carbon cycling in the mesopelagic (Silver et al. 1998; Robison et al., 2005b). The UVP produces vertical profiles of the size distribution of large particles, and so allows the determination of the decrease in the vertical mass flux with depth (Guidi et al., 2009). New technologies also mean that it is possible to sample at a selected depth without disturbing fine vertical structures such as subsurface particle maxima. The Free-falling Imaging Device for Observing phytoplankton (FIDO-Φ) of Franks and Jaffe (2007), the SMAST T-REMUS autonomous underwater vehicle of Wang and Goodman (2009), and the FSS (Fine Scale Sampler) of Lunven et al. (2005), are examples of instrumentation that could be developed for mesopelagic research.

The recent development of a PArticles Sinking Simulator (PASS) allowed Tamburini et al. (2009) to perform experiments at increasing hydrostatic pressure on both diatom detritus derived from an axenic culture (Tamburini et al., 2006) and freshly collected fecal pellets incubated with natural microbial assemblages. Increasing experimental pressure simulated the

sinking of particles through the water column and demonstrated a pressure effect on aminopeptidase activity, silicic acid regeneration, and degradation of organic matter, rather than on the prokaryotic community structure.

Stable isotopes show a stepwise enrichment from prey to predator and thus allow the relative trophic position of a species within a foodweb to be established. Fatty acids, distinctive of different prey, that accumulate in predators' tissues, can be used as biomarkers of feeding history. The combination of these two techniques has recently been used to distinguish carbon sources between diatoms and other phytoplankton (Budge et al., 2008), and to investigate the trophic ecology of deep-sea fish (Stowasser et al., 2009).

The application of environmental genomics to the mesopelagic zone has identified some of the genes and metabolic pathways present. This has led to unexpected insights into the diversity of microbes and microbial processes which regulate local and global elemental cycles (DeLong and Karl, 2005; Zak et al., 2006; Hamersley et al., 2007; Reinthaler et al., 2010).

7. Future directions

A strategy to improve our knowledge of the biogeochemical and ecological interactions in the mesopelagic layer and predict how these may change in the future must encompass novel methodologies to sample the biota at representative time and space scales including fine-scale vertical resolution, diel variability and episodic events. Sampling methods should take into account pressure effects, the potential for non-random distribution of microbes (Azam and Malfatti, 2007) and metazoans, and the fragility of many taxa. The use of autonomous vehicles and floats, long-term deepwater observatories, in situ video systems and novel biogeochemical and molecular tracers will be required.

Studies that have statistically compared the relationship between environmental parameters, community structure and biogeochemical processing are few, and have focused on prokaryotic communities in the euphotic zone (Reinthaler et al., 2005; Alonso-Sáez et al., 2007). These comparative studies should be extended to the mesopelagic.

Modeling has a central role to play in helping us understand the roles of the diverse array of organisms that inhabit the mesopelagic zone in consuming and processing organic matter. Models offer a framework in which the ramifications of existing knowledge can be articulated, providing explicit quantitative descriptions of what we do and do not understand (Gasol et al., 2008; Anderson, in press). Simple flow analysis models may be used to address some of the most basic unknowns e.g. the relative contributions of microbes and zooplankton in attenuating and respiring POC within the mesopelagic zone. More complex models (e.g., Jackson and Burd, 2002; Stemmann et al., 2004b) that resolve vertical distributions of animals, detailed structure and diversity within the food web (e.g., Le Quéré et al., 2005) and the resulting impact on the transformations of particulate and dissolved organic matter within the water column, are also needed. Such models require intensive field programmes to provide the data necessary for model validation.

7.1. Community structure

Future research should improve characterisation of the distribution, diversity and activity (e.g., feeding rates and metabolic demands) of the groups which have thus far proved too difficult to study, yet which may have a disproportionate impact on our understanding of carbon cycling e.g. gelatinous zooplankton, microzooplankton, archaea, viruses, and fish. There

are still large gaps in our knowledge of mesopelagic microbial and metazoan community structure, including undiscovered species, and unknown abundances of known species.

Little is known about the abundance, biomass, and activity of bacterial predators and competitors such as heterotrophic nanoflagellates, ciliates, heterotrophic dinoflagellates, foraminifera, viruses and fungi (e.g., Tanaka and Rassoulzadegan, 2002; Yamaguchi et al., 2002; Steinberg et al., 2008b). Studies with submersibles and other underwater video systems indicate gelatinous zooplankton are conspicuous, abundant members of the mesopelagic community (e.g., Silguero and Robison, 2000; Stemmann et al., 2008), but the role that many of these animals play in carbon and energy transfer in the mesopelagic is unknown. The asexual stage in the life history of many gelatinous zooplankton taxa allows rapid reproduction and formation of high density 'blooms' in surface waters, and the fate of these blooms as animals die and sink through the mesopelagic may be to fuel higher trophic level (and benthic) production (Billet et al., 2006). Large increases in gelatinous zooplankton have been observed worldwide in coastal, surface waters (Mills, 2001), but long-term changes in mesopelagic gelatinous zooplankton abundance are unknown.

7.2. Foodweb dynamics

An important question that remains to be resolved is whether or not the mesopelagic foodweb is fundamentally different from that in the euphotic zone. The microbial loop in the mesopelagic realm is not well understood. Specialized zooplankton (e.g., appendicularians and salps) that consume particles as small as bacteria, or omnivorous mesozooplankton feeding on aggregates and marine snow containing microbes, can 'short circuit' trophic steps between microbes, primary producers and mesozooplankton. Recent data on changes in the relative abundance of prokaryotes, flagellates and viruses with increasing depth suggest that either viruses and flagellates behave fundamentally differently at depth, or that bacterivory and viral infection occur predominantly associated with colloidal or particulate matter (Herndl et al., 2008). Models, underpinned with targeted data, will need to take these mesopelagic trophic interactions into account.

7.3. Ecological interactions with dissolved organic material

Much remains to be learnt about how the complex microscale architecture of DOM in seawater, including tangled webs of colloids, gels, mucous sheets and bundles, contributes to the heterogeneity of nutrient supply and thus microbial abundance and diversity (Azam and Malfatti, 2007). Excretion of DOM by mesopelagic zooplankton may provide a high-quality substrate for bacteria at depth (Steinberg et al., 2008a). Experiments are needed to characterize this zooplankton-derived DOM and measure its uptake by mesopelagic microbes. Correlative data suggest correspondence between DOM quality and heterotrophic bacterial activity and community structure, however direct links between specific natural organic compounds and specific microbial lineages and activity is still lacking. Much of this is due to the methodological limitations of identifying a significant fraction of the organic compounds that comprise the DOC pool. Progress has been made in developing indices of lability (Skoog and Benner, 1997; Amon et al., 2001; Benner, 2002) and there is emerging potential to use high resolution mass spectrometry (Kujawinski and Behn, 2006) to reveal the effect of microbial processes on the production and removal of specific compounds. These techniques in combination with genomic, transcriptomic and proteomic approaches may yield the valuable data needed to make explicit

linkages between specific resource use and the organism(s) responsible for its use.

7.4. Ecological interactions with particulate material

Understanding the differences in physiology and ecology of free-living prokaryotes and those associated with suspended materials, e.g. in terms of substrate affinity and growth efficiency, is important for determining their relative contributions to the turnover of organic carbon and the carbon budget of the mesopelagic zone (Anderson and Tang, 2010). Improved understanding of the degradation, fragmentation and repackaging of sinking aggregates will allow the biological pump to be included in global models as more than simply an empirically-determined decline in POC concentration with depth (De La Rocha and Passow, 2007). Key areas needing work are the amount of POC flux associated with appendicularians, the mechanisms by which coccoliths and coccolithophorid POC reach depth, and the impact of polymers such as TEP on the porosity of aggregates (De La Rocha and Passow, 2007).

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