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Analyzing the trophic link between the mesopelagic microbial loop and zooplankton from observed depth profiles of bacteria and protozoa

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Abstract. It is widely recognized that organic carbon exported to the ocean aphotic layer is significantly consumed by heterotrophic organisms such as bacteria and zooplankton in the mesopelagic layer. However, very little is known for the trophic link between bacteria and zooplankton or the function of the microbial loop in this layer. In the northwestern Mediterranean, recent studies have shown that viruses, bacteria, heterotrophic nanoflagellates, and ciliates distribute down to 2000 m with group-specific depth-dependent decreases, and that bacterial production decreases with depth down to 1000 m. Here we show that such data can be analyzed using a simple steady-state food chain model to quantify the carbon flow from bacteria to zooplankton over the mesopelagic layer. The model indicates that bacterial mortality by viruses is similar to or 1.5 times greater than that by heterotrophic nanoflagellates, and that heterotrophic nanoflagellates transfer little of bacterial production to higher trophic levels.

1 Introduction

The current view of ocean biogeochemistry is that organic carbon (OC) exported from the euphotic layer is mostly remineralized in the mesopelagic layer, otherwise considered buried in the ocean interior (e.g. Fowler and Knauer, 1986). While sinking particulate organic carbon (POC) is consumed by particle-attached bacteria and detritivorous zooplankton during the sinking process (Martin et al., 1987; Cho and Azam, 1988; Smith et al., 1992), dissolved organic carbon (DOC), which is exported from the euphotic layer or released from sinking POC, is accessible only for free-living bacteria. However the trophic link between bacteria and zooplankton, i.e. the structure and function of the microbial loop, is unknown in the mesopelagic layer, by which our understanding of biological process in global material cycling may be limited.

Recent studies in the northwestern Mediterranean reported vertical and seasonal variations in abundance of viruses, bacteria, heterotrophic nanoflagellates (HNF), and ciliates, and of bacterial production, in the aphotic layers down to 2000 m (Harris et al., 2001; Tamburini et al., 2002; Tanaka and Rassoulzadegan, 2002; Weinbauer et al., 2003). In addition, Tanaka and Rassoulzadegan (2004) showed that bacteria at 500 m were controlled by both bottom-up (substrate) and top-down (predation) controls. In this paper, we analyzed carbon flow in the mesopelagic microbial loop-zooplankton, using the published data combined with a simple steady-state food chain model. Results indicated that bacterial mortality by viruses is similar to or 1.5 times greater than that by HNF, and that HNF transfer little of bacterial production to higher trophic levels.

2 Study site

The data used in this study were obtained at the French-JGOFS time-series station DYFAMED (43°25.2′ N, 07°51.8′ E; 2350 m max depth) in the northwestern Mediterranean, and have been published in Tanaka and Rassoulzadegan (2002, 2004, see also for detailed description of materials and methods). This site is likely independent of anthropogenic and natural dust inputs (Marty et al., 1994; Ridame and Guieu, 2002) and receives very weak lateral flows (Béthoux et al., 1988; Andersen and Prieur, 2000). Water temperature is always ca. 13°C below seasonal thermocline down to 2000 m during the stratified period and in whole water column during the mixing period, and no permanent pycnocline exists (Marty, 2003). This site shows contrasted seasonal patterns of water column structure and biological production in the upper layer (Marty and Chiavérini, 2002), with

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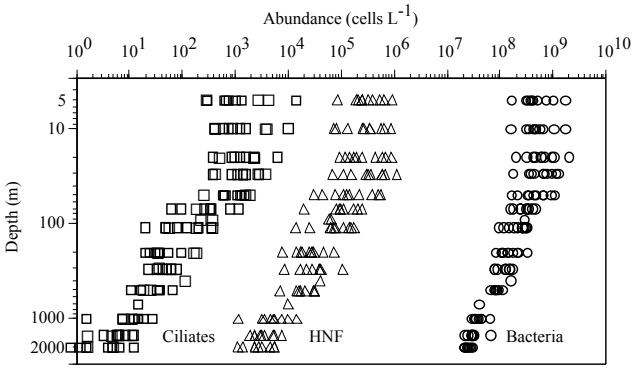

Fig. 1. Distributions of bacteria, heterotrophic nanoflagellates (HNF) and ciliates. Measurements were monthly done at 13 depths between 5 and 2000 m from May 1999 to March 2000 at the DYFAMED site (Redrawn from Tanaka and Rassoulzadegan, 2002). Circles, triangles and squares denote bacteria, HNF and ciliates, respectively.

the consequence that sinking POC fluxes are higher from January to June and smaller from July to December (Miquel et al., 1993, 1994) and that DOC is accumulated in the surface mixed layer during the stratified period and exported during the winter mixing period (Copin-Montégut and Avril, 1993; Avril, 2002). Annual fluxes of sinking POC between 100 and 1000 m are estimated to be 0.4 mol-C m^{-2} yr^{-1} (Miquel et al., 1994). The depth of the winter vertical mixing (<1000 m) and relatively stable DOC concentrations in the deeper layer (1000–2000 m) suggest that most of the DOC exported from the euphotic layer (1-1.5 mol-C m^{-2} yr^{-1}) is consumed in the upper 1000 m (Copin-Montégut and Avril, 1993; Avril, 2002). These fluxes between 100 and 1000 m correspond to 75% of sinking POC and ∼100% of exported DOC from the euphotic layer. It is reported that sinking POC was consumed by detritivorous zooplankton (Carroll et al., 1998) and particle-attached bacteria (Turley and Stutt, 2000) during the sinking process at the same site.

3 Background of the aphotic microbial heterotrophs at the study site

Tanaka and Rassoulzadegan (2002) demonstrated that bacteria, HNF and ciliates were always detected throughout the water column during an annual study, with one, two and three orders of magnitude of depth-dependent decrease (5–2000 m), respectively, at the DYFAMED site (Fig. 1). Regardless of greater seasonal variations in abundance in upper layer, the log-log linear regression analysis for abundance vs. depth showed that the regression slope values (the index of magnitude of depth-dependent decrease) were relatively constant for each group, and that the depth-dependent decreases of abundance were significantly smaller for bacteria than protozoa, by which the biomass contribution of bacteria to total microbial heterotrophs increased from 60 to 95% with depth (Tanaka and Rassoulzadegan, 2002). Under the assumption that the food web was close to steady state, this suggests that rate processes (i.e. growth and loss rates) are less variable for bacteria than for protozoa over the depth, and that the density-dependent predator-prey relationship becomes less coupled between the three microbial heterotrophs with increasing depth down to 2000 m.

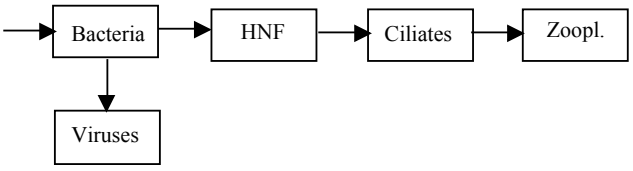

Fig. 2. Flow structure of the model used for analyzing carbon flow in the mesopelagic layer of the northwestern Mediterranean. The model consists of viruses, bacteria, heterotrophic nanoflagellates (HNF), ciliates, and zooplankton.

A following study at the same site showed that while bacterial biomass and production showed depth-dependent decreases over the 110–1000 m layer, both parameters were seasonally variable down to 300 m and 500 m, respectively (Tanaka and Rassoulzadegan, 2004). The comparison in changing rate of bacterial abundance in different treatments (whole water from 500 m, predator-free water from 500 m, predator-free water from 500 m diluted by particle-free water from 500 m, and predator-free water from 500 m diluted by particle-free water from 110 m) suggested that bacteria at 500 m were controlled by both bottom-up (substrate) and top-down (predation) controls, and that the availability of dissolved organic matter was seasonally variable down to 500 m (Tanaka and Rassoulzadegan, 2004). In the 1000–2000 m, bacterial production showed seasonal variations but did not decrease with depth (Tamburini et al., 2002).

4 Model

Our knowledge of the structure and function of the microbial loop is quite limited for the aphotic layer due to the scarcity of direct measurements of biomass and rate process. If one assumes a food-web structure for carbon flow, and combines this with the assumption of an approximate steady state over the depths (e.g. Thingstad, 2000), the data on biomass of microbial heterotrophs and bacterial production can be used to estimate carbon flows between microbial heterotrophs and zooplankton over the mesopelagic layer (hereafter 110–1000 m). We assumed a simple food chain of viruses, bacteria, HNF, ciliates and zooplankton, in which only bacteria have two loss processes (viruses and HNF) (Fig. 2). An expression for the observed level of bacterial biomass can be obtained by using the steady state requirement for HNF at biomass H (nmol-C L^{-1}), eating bacteria at

Table 1. Estimated parameter values in Eqs. (4) and (5) based on a linear regression model I.

Variables (x, y)	Model	Slope (±SE)	Slope significance	Y-int. (±SE)	Y-int. significance	n	r^2
H^*, BP/B^*	$y=\alpha_H x+\delta_{BV}$	0.0007±0.0001	$P<0.0001$	0.0069±0.002	$P=0.0015$	29	0.467
10 B^*, C^*	$y=Y_H x$	0.0112±0.0015	$P<0.01$			5	0.949

biomass B (nmol-C L^{-1}) with a specific clearance rate of α_H (L nmol-C^{-1} d^{-1}) and a yield of Y_H (no dimension), and that for viruses with a specific loss rate δ_{BV} (d^{-1}). The specific loss rate of bacteria by viruses is adapted in order to compromise with limited data on viruses. The number of bacterial prey caught per unit time per unit predator is assumed to be proportional to prey abundance (α_H B), the total loss due to predation is then α_H B H. Total loss of bacteria by viruses can be given by δ_{BV} B. At steady state, production of new bacterial biomass (BP: nmol-C L^{-1} d^{-1}) balances the total loss, that is:

$$BP = \alpha_H \; B^* H^* + \delta_{BV} \; B^*, \tag{1}$$

where the asterisk denotes steady state biomass of predator and prey. Likewise, the observed level of HNF biomass can be obtained by using the steady state requirement for ciliates at biomass C (nmol-C L^{-1}), eating HNF at biomass H with a specific clearance rate of α_C (L nmol-C^{-1} d^{-1}) and a yield of Y_C (no dimension). Then, the production of new HNF biomass $Y_H \alpha_H$ B H balances the loss to ciliates $\alpha_C H$ C, that is:

$$Y_H \alpha_H B^* H^* = \alpha_C \; H^* C^*. \tag{2}$$

If we introduce a specific loss rate of ciliates by zooplankton as δ_{CZ} (d^{-1}) due to limited data on zooplankton, the production of new ciliates biomass $Y_C \alpha_C H$ C balances the loss to zooplankton $\delta_{CZ} C$, that is:

$$Y_C \alpha_C H^* C^* = \delta_{CZ} \; C^*. \tag{3}$$

Arranging Eq. (1) gives:

$$BP/B^* = \alpha_H H^* + \delta_{BV}. \tag{4}$$

Linear regression of Eq. (4) with the data of H^* and BP/B^* allows direct estimates of α_H and δ_{BV}. Growth yield is considered variable with environmental conditions, and no data are available for the mesopelagic HNF and ciliates. Clearance rate is considered to be a function of prey density, which is assumed to be valid in the aphotic layer. Increase in cell size of the mesopelagic bacteria was not recognized under microscopic observation (Tanaka, personal observation). It is reported that specific clearance rate of bacterivorous HNF was ~10 times greater than that of ciliates preying on small particles in the euphotic layer (Fenchel, 1987). Under the assumption of α_C=0.1 α_H, Eq. (2) is arranged as:

$$C^* = Y_H \; (10 B^*). \tag{5}$$

Linear regression of Eq. (5) with the data of B^* multiplied by 10 and C^* allows direct estimate of Y_H. Y_C was arbitrarily assumed equal to Y_H. Because the biomass of HNF and ciliates was not measured simultaneously with bacterial production (see Tanaka and Rassoulzadegan, 2002, 2004), we used annual mean values in biomass of bacteria, HNF and ciliates obtained in 1999–2000, but the depths correspond to those of bacterial production.

Using the estimated parameters combined with the annual mean of integrated biomass of bacteria, HNF and ciliates, carbon flows between the microbial heterotrophs and zooplankton were estimated over the mesopelagic layer: $\delta_{BV} B^*$ from bacteria to viruses, $\alpha_H B^* H^*$ from bacteria to HNF, $\alpha_C H^* C^*$ from HNF to ciliates, and Y_C $\alpha_C H^* C^*$ from ciliates to zooplankton. Error estimates in the carbon flow were evaluated by taking into account standard errors (SE) of the regression slopes (α_H and Y_H) and of the regression intercept (δ_{BV}).

5 Results and discussion

Significant linear regressions were obtained in both Eqs. (4) and (5), while the coefficient of regression was not high for Eq. (4) (Table 1; Fig. 3). Specific clearance rate (±SE) of HNF for bacteria was estimated to be 0.0007±0.0001 L nmol-C^{-1} d^{-1} over the 110–1000 m. Based on measurement of uptake rates of fluorescently labeled bacteria by HNF, Cho et al. (2000) reported that HNF clearance rates ranged from 1 to 11 nL HNF^{-1} h^{-1} in the upper 500 m of the East Sea. By using the mean cell volume of 20 μm^3 HNF^{-1} in the mesopelagic layer of our study site (Tanaka and Rassoulzadegan, 2002) and a carbon to volume conversion factor of 183 fg C μm^{-3} (Caron et al., 1995), the above range of clearance rates is transformed to the carbon-based specific clearance rate as 0.00008 to 0.0009 L nmol-C^{-1} d^{-1}. Our estimate is in the upper part of this range. HNF growth efficiency on bacteria was estimated to be 1.12 (±0.15)%. This estimate is sensitive to the assumption of the ratio of ciliates to HNF specific clearance rate in our model. Instead of the original assumption made, if we assume that specific clearance rate is as high for ciliates as HNF, or as low for HNF as ciliates (i.e. α_C=α_H), HNF growth efficiency is estimated to be 11.2 (±1.5)%. Ranges of growth efficiency measured under variable experimental conditions (e.g. temperature and prey concentration) were from 4 to 49% for flagellates and from 2 to 82% for ciliates

Table 2. Carbon flow estimates for the mesopelagic layer (110–1000 m), which are based on the estimated parameters (±SE) of α_H (0.0007±0.0001), Y_H (0.0112±0.0015), δ_{BV} (0.0069±0.002). Data on annual mean biomass are from Tanaka and Rassoulzadegan (2002).

	Mean biomass (mmol-C m^{-2})	Carbon flow (±SE) (mmol-C m^{-2} yr^{-1})
Bacteria	130	327 (±95) (to viruses) 249 (±36) (to HNF)
HNF	6.7	2.2 (±0.32) (to ciliates)
Ciliates	11.7	0.025 (±0.007) (to zooplankton)

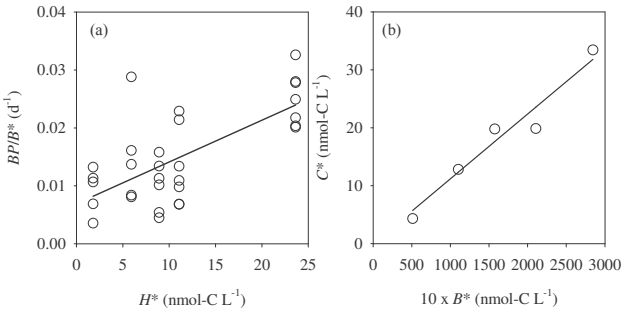

Fig. 3. Rate estimations by fitting the model-derived equations. **(a)** Relationship between BP/B^* and H^*, **(b)** Relationship between C^* and 10 B^* in the 110–1000 m. BP, B, H and C denote bacterial production, biomass of bacteria, heterotrophic nanoflagellates and ciliates, respectively. The asterisk denotes steady state biomass. Data on biomass and bacterial production are from Tanaka and Rassoulzadegan (2002) and Tanaka and Rassoulzadegan (2004), respectively. The lines were calculated with a linear regression model I (Table 1).

(reviewed by Caron and Goldman, 1990). A barophilic flagellate isolated from 4500 m depth sediments showed 17–25% of growth efficiency under the condition of bacterial preys on the order of 10^{10} cells L^{-1} enriched with sterilized phytodetritus (Turley et al., 1988). Our estimates are in the lower end of or smaller than the reported ranges. Under the assumption that the study site is in an approximate steady-state over multiyear in terms of OC stock and that most of OC remineralization can be attributed to bacteria in the mesopelagic layer, bacterial growth efficiency has been estimated to be 19–39% on an annual scale, by replacing a total amount of OC assimilated by bacteria with the OC flux between 110 and 1000 m (Tanaka and Rassoulzadegan, 2004). This may suggest that the bacterial ingestion by HNF functions as remineralization rather than energy transfer to higher trophic levels. It has been demonstrated that HNF can release a significant fraction of ingested prey as dissolved organic matter (reviewed by Nagata, 2000). Although no data on HNF respiration and egestion are available for the mesopelagic layer, the OC egestion by HNF seems to be less significant in the OC-limited condition.

A back-calculation, using the estimated parameters and the annual mean of integrated biomass, suggests that 40–48% of bacterial mortality is due to HNF predation and the rest due to viruses over the mesopelagic layer (Table 2). This however may be contrary to a recent suggestion that virus-induced mortality of bacteria is low (3–6%) in the mesopelagic and bathypelagic layers at the same site (Weinbauer et al., 2003). Because the empirical model to estimate virus-induced mortality of bacteria is not derived from mesopelagic and bathypelagic layers and data on virus-induced mortality of bacteria in the ocean aphotic layer have been limited to this study site (Weinbauer et al., 2003), it may be difficult to validate these estimates at present. Of total bacterial production that is equivalent to bacterial mortality by viruses and HNF, 0.36–0.43% and 0.0039–0.0046% are transferred to ciliates and zooplankton, respectively. Another assumption (α_C=α_H) results in slightly higher transfer of bacterial production to ciliates (3.6–4.3%) and zooplankton (0.39–0.46%). This suggests a distance of the trophic link between "viruses, bacteria and HNF" and "ciliates and zooplankton". Conceptually, specialized zooplankton (e.g. appendicularians and salps) that can consume particles as small as bacteria may reduce this distance by making a shortcut between the microbial loop and zooplankton. The observation of pellet fluxes at 500 m at the study site suggested the presence of mesopelagic appendicularians (Carroll et al., 1998), which were dominant in the macrozooplankton community around 400 m near the study site (Laval et al., 1989). Due to the paucity of data on zooplankton distribution and feeding, effect of such specialized zooplankton on our model remains to be open. Precision in our estimates of carbon flow may have suffered from the relatively low precision in microscope-based biomass estimates.

Increase in number of trophic levels generally results in less efficient material transfer from lower to higher trophic levels or more efficient remineralization in the food web, which has been addressed as a function of the microbial loop in the euphotic layer (Azam et al., 1983). This context may be reflected in the mesopelagic layer, where all microbial heterotrophs and zooplankton exist and constitute the mesopelagic food chain. Our model analysis suggests that the mesopelagic bacterial production is similarly allocated to "DOC-bacteria-viruses" circuit and "DOC-microbial loop" circuit, or 1.5 times greater to the former than the latter, and that HNF are potentially important remineralizers of the mesopelagic bacterial production.

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