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Major constrains of the pelagic food web efficiency in the Mediterranean Sea

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Abstract

Grazing pressure plays a key role on plankton communities affecting their biodiversity and shaping their structures. Predation exerted by 2–200 µm protists (i.e. microzooplankton and heterotrophic nanoplankton) influences the carbon fate in marine environments channeling new organic matter from the microbial loop toward the “classic” grazing food web.

In this study, we analyzed more than 80 dilution experiments carried out in many Mediterranean sites at the surface and in the meso-bathypelagic layers. Our aims were to investigate prey-predator interactions and determine selectivity among energy sources (in terms of available biomass), efficiency in the exploitation and highlight likely constraints that can modulate carbon transfer processes within the pelagic food webs.

Generally, microzooplankton shown higher impacts on prey stocks than heterotrophic nanoflagellates, expressing larger ingestion rates and efficiency. Through different trophic conditions characterized on the base of chlorophyll *a* concentration, microzooplankton diet has shown to change in prey compositions: nano- and picoplankton almost completely covered consumer needs in oligotrophy and mesotrophy, while microphytoplankton (mostly diatoms) represented more than 80 % of the consumers' diet in eutrophy, where, nevertheless, picoplankton mortality remained relatively high.

Ingestion rates of both consumers (nano- and microzooplankters) increased with the availability of prey biomasses and consequently with the trophic condition of the environment. Nevertheless, overall the heterotrophic fraction of picoplankton resulted the most exploited biomass by both classes of consumers.

Ingestion efficiency (as the ratio between available biomass and ingestion rate) increased at low biomasses and therefore the highest efficiencies were recorded in oligotrophic conditions and in the bathypelagic layers.

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1 Introduction

The “classic” marine pelagic food web was firstly introduced by Ryther (1969) to predict fish production, and links phytoplankton to the nekton through zooplankton grazing. Several conceptual models were developed to cover different scenarios from upwelling areas with fish diet based on large phyto- and zooplankton to oceanic waters with small phytoplanktonic cells and several trophic levels before fishes.

Since early 80’s Azam et al. (1983) drastically evolved this view introducing the microbial loop model that posed bacteria at the base of the food webs. Microbes are responsible for nutrient uptake and organic matter remineralisation; their biomass partly replenishes the bulk of dissolved organic matter (through exudation and lysis) and partially is transferred to the upper trophic levels.

At the surface, the major consumers belonging to the microbial domain are heterotrophic protists and larval stages of metazoans with dimensions ranging from 2 to 200 μm , here considered as Microzooplankton (MZP; 10–200 μm) and Heterotrophic nanoflagellates (HNF; 2–10 μm). Grazing of MZP and HNF on smaller organisms is critical for the carbon transfer along the trophic food web and for the remineralisation of organic carbon (Sherr and Sherr, 1994). Planktonic communities are also structured by grazing pressure that controls their biomass, diversity (James and Hall, 1998; Lessard and Murrell, 1998), and primary productivity (Burkhill et al., 1995; Cotano et al., 1998).

In the aphotic zone, despite it accounts for 70 % of total seawater volume, food webs are almost unexplored (Nagata et al., 2010). Deep-water communities were generally considered bottom-up controlled because picoplankton and consumers (MZP and HNF) tend to decrease in abundances by 2–3 orders of magnitude (Reinthal et al., 2006), which implies a drastic reduction of the grazing pressure. However, picoplankton have a non-random distribution because the organisms tend to live attached to sinking particles creating micro-hot spots (Azam, 1998; Herndl et al., 2008; Aristegui et al., 2009; Nagata et al., 2010). Aristegui et al. (2009) reevaluated the significance of grazing and found that HNF-prey ratio only halves in meso-bathypelagic zones from the eu-

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photic ratio. MZP grazing is almost negligible due to dilution effect, and the relevance of viral-induced mortality is still unclear: Fonda Umani et al. (2010) found that viral induced mortality affected heterotrophic picoplankton on average 4 times less than HNF grazing (even with significant differences among Mediterranean regions), while Parada et al. (2007) found that in the bathypelagic realm virus-host ratio increase by 10 \times relative to the surface in North Atlantic.

The assessment of the predators' grazing pressure on prokaryotes is a key point in order to understand the efficiency of the food webs in the carbon flux in marine pelagic environments. Landry and Hassett (1982) introduced decades ago the dilution technique, considered now a standard protocol (Dolan et al., 2000), to estimate ingestion rates of MZP and HNF, and potential production of preys. The technique was based on the analysis of chlorophyll *a* concentration as a proxy for prey's biomass that at that time considered only the autotrophic fractions. Other authors reached higher resolution assessing ingestion rates and potential production for different classes of preys through pigment analysis (HPLC, flow cytometry), counts at the microscope of micro-phytoplankton, counts in epifluorescence microscopy of autotrophic and heterotrophic nano- and picoplankton (e.g. Fonda Umani and Beran, 2003; Fonda Umani et al., 2005, 2010, 2012; Modig and Franze, 2009; Gutiérrez-Rodríguez et al., 2010, 2011; Lie and Wong, 2010; Selph et al., 2011; Di Poi et al., 2013; Latasa et al., 2014; Liu et al., 2014). HNF were found to heavily exploit picoplanktonic communities at the surface (Tsai et al., 2012) and represent the largest source of prokaryotic mortality in the bathypelagic system (Fonda et al., 2010), however Calbet and Landry (2004) assessed that MZP have the highest exploiting efficiency among surface consumers, handling on average 2/3 of the primary production and leaving the remaining to larger consumers, viral lysis, export or circulation losses. Several authors pointed out as MZP represent the principal grazers of phytoplankton (Banse, 1995) in oligotrophic regions of the oceans and it might be true even in upwelling and coastal areas (Calbet, 2001; Calbet and Landry, 2004).

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Oligotrophic regions are usually microbial food web dominated due to prokaryotes' ability to outcompete larger organisms for nutrient uptakes and they represent the major source of organic carbon. The "classic" grazing food web predominates in meso- and eutrophic conditions when fresh supply of land derived mineral nutrients or upwelling events increase nutrient availability; the latter condition supports the growth of larger phytoplankton that became the principal supplying source for large consumers (Fenchel, 2008).

However, De Leander et al. (2010) using the linear inverse model approach, estimated that in microbial dominated trophic food webs bacteria are four time more important than phytoplankton in the protists' diet while in herbivorous dominated food webs the diet of protists consist of similar amounts of bacteria and phytoplankton.

Considering all together the primary producers (autotrophic micro-, nano- and picoplankton) their respective mortality rates induced by grazing of MZP and HNF are still relatively scarcely estimated (Reckermann et al., 1997; Calbet et al., 2008; Modigh and Franz, 2009; Lie and Wong, 2010; Gutiérrez-Rodríguez et al., 2010, 2011; Selph et al., 2011; Liu et al., 2014; Latasa et al., 2014). The grazing efficiency of consumers on the heterotrophic nano- and picoplankton is poorly or even understudied (Tsai et al., 2012; Fonda Umani et al., 2012; Di Poi et al., 2013) and it is definitely worse in the meso- and bathypelagic domains (Fonda Umani et al., 2010). For freshwater environments few studies indicated a selective feeding on cyanobacteria as well as on heterotrophic bacteria (Domaizon et al., 2003; Tijdens et al., 2008; Personnic et al., 2009; Burian et al., 2013; Tsai et al., 2015).

The main aims of this study was to determine (i) the significance of prokaryotic biomass in MZP and HNF diet, (ii) the efficiency of the pelagic food webs throughout the entire Mediterranean Sea, (iii) the major constrains that modulate the efficiency of Carbon transfer toward upper trophic levels.

We used the results of a large dataset of dilution experiments (partially already published – Fonda Umani et al., 2010, 2012; Di Poi et al., 2013 and partially unpublished)

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carried out in the entire Mediterranean Sea that have assessed MZP and HNF predation rates on several prey classes.

The Mediterranean Sea is considered an oligotrophic basin due to the scarce pool of nutrients and chlorophyll *a* (Krom et al., 1991; Antoine et al., 1995). Oligotrophy 5 exasperates moving eastwards as remarked by major decreasing gradients of nutrient concentrations (Krom et al., 1993), primary production, autotrophic biomass, export of primary production (Danovaro et al., 1999; Dolan et al., 1999; Turley et al., 2000) and chlorophyll concentration (Williams, 1998).

On average, the most limiting nutrient is inorganic phosphorus, N : P ratio was found 10 up to 60, while carbon and nitrogen limitations can occur and co-occur and they are influenced by depth (Sala et al., 2002; Van Wambeke et al., 2000, 2009). Phosphorus limits the primary production (Berland et al., 1984; Thingstad and Rassoulzadegan, 1995, 1999; Thingstad et al., 2005) but while phytoplankton are both N and P limited, picoplanktonic portion is more sensitive to P limitation (Pitta et al., 2005; Thingstad 15 et al., 2005; Zohary et al., 2005). This depleted condition tightly affects communities that populate the Mediterranean ecosystems whose food webs are mostly microbes-dominated (Wikner and Hagström, 1988; Fogg, 1995).

In the Mediterranean Sea and in other oligotrophic environments, picoplankton activity represents the most important trophic step (Williams, 1984). Prokaryotic growth 20 efficiency was found to be inversely correlated with C : N ratio therefore the biomass and the amount of carbon flux related with picoplankton compartment are larger in oligotrophic areas (Biddanda et al., 1994). As the trophic status increases, picoplankton biomass increases at a lower ratio in comparison to microphytoplankton biomass (Williams, 1984; del Giorgio et al., 1997; Cole, 1999).

25 Some areas of the basin (close to river mouths, upwelling areas) characterized by eutrophic conditions present plankton communities where larger autotrophic and heterotrophic organisms become more representative; Biddanda et al. (2001) remarked as in these regions picoplanktonic respiration is a small percentage of total plankton respiration.

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2 Materials and methods

2.1 Studied areas

Experiments were performed at 15 sites spread around the Mediterranean Sea. Specifically, from east to west: Aegean Sea (3 sites), Ionian Sea (3 sites), Otranto strait (1 site), Adriatic Sea (3 sites), Tyrrhenian Sea (1 site), Ligurian Sea (1 site), Balearic Sea (1 site), Alboran Sea (1 site) and Atlantic Ocean (1 site) (Fig. 1).

At these sites 82 dilution experiments were set up: 68 carried out at the sub-surface level (-0.5 m) and 14 carried out at in the meso-bathypelagic realm (between 670 and 3860 m of depth). Among the surface experiments, 34 were designed to assess the grazing pressure of MZP and 34 targeted the grazing pressure of HNF.

Experiments were performed on board during two oceanographic cruises: Transmed campaign of the VECTOR project, from 28 May to 28 June 2007 on board of the R/V *Urania* and *Universitatis* (9 sites along a west to east transect); OBAMA cruise of the namesake project, from 24 March to 6 April 2011 on board of the R/V *Urania* (5 sites between the Northern Ionian Sea and the Southern Adriatic Sea). Details of the sampling are reported in appendix Table A1 and A2.

Water samples were seasonally collected at the station C1 (13.710° E, 45.701° N, depth 17 m) in the Gulf of Trieste – Northern Adriatic Sea from autumn 1998 to summer 2005 to set up the dilution experiments that were run under in situ simulated conditions at the Laboratory of Marine Biology of Trieste, Italy (now Department of Biological Oceanography, BiO, OGS, Trieste, Italy). A total of 42 experiments were analysed giving a description of the lower part of the pelagic food web in a coastal area during eutrophic, mesotrophic and few oligotrophic conditions (for more details see Fonda Umani et al., 2005, 2012).

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2.2 Dilution techniques

Dilutions experiment (MZP). Forty-eight liters of seawater were collected at the surface layer and filtered immediately on a 200 μm mesh to remove larger predators. Two identical bottle sets (2 L) of four dilutions each were made in the following proportions:

- 5 100 % (whole water), 80, 50 and 10 % in three replicates each. Part of the collected seawater was filtered on a 0.22 μm membrane and used to dilute the samples. The first set of dilutions (T_0) was immediately fixed with buffered and filtered formaldehyde solution (2 % final concentration). The second set of dilution (T_{24}) amended with nutrients (5 μM NaNO₃ and 1 μM KH₂PO₄), was incubated at in situ temperature for 24 h under
- 10 natural light conditions (flow-through system aquarium). At the end of the incubation, the samples were also fixed. Samples for MZP and microphytoplankton analyses were conserved in plastic bottles and at ambient temperature, while samples for nanoplankton and picoplankton analyses were conserved in black plastic bottles, stored in the dark and at 4 °C, until the laboratory analysis.

- 15 *Dilutions experiment (HNF).* Twelve liters of seawater were collected at the surface as well as in the meso-bathypelagic layers, pre-filtered immediately on a 200 μm mesh and then filtered on a 10 μm mesh to remove larger predators. Sets of dilutions were prepared as for MZP sets on 500 mL bottles. Sets for experiments with meso- and bathypelagic layer communities were incubated at in situ temperature for 24 h in the dark in a portable fridge. Samples were fixed and stored as described before.

At each sampling event sea water used for both MZP and HNF dilution experiments was simultaneously collected.

- 25 Based on the dilution method model I of Landry and Hassett (1982) modified by Landry et al. (1995), we computed for several classes of prey (microphytoplankton, nanoplankton, heterotrophic and autotrophic picoplankton): growth factor (μ), grazing factor (g), initial concentration of the prey (C_0), mean concentration of the prey during

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the experiment

$$[C_m = C_0(e^{(\mu-g)t} - 1)/(\mu - g)t] \quad (1)$$

$$\text{ingestion rate } [I = g \times C_m], \quad (2)$$

$$\text{potential production } [P_P = \mu \times C_m]. \quad (3)$$

5 2.3 Microscopic analysis and cell to biomass conversion factors

Micro-plankton. Samples for microphytoplankton and MZP were processed following the Utermöhl method (1958), organisms were enumerated and measured using an inverted optical microscope. Cell numbers of ciliates were corrected multiplying them by 1.56 in order to compensate possible loss of organisms due to the fixation with formaldehyde (Stoecker et al., 1994a, b).

Taxonomic assignations, standardized geometrical formulas for volume conversion and carbon conversion factor were done following Strathmann (1967) and Smayda (1978) for microphytoplankton, Putt and Stoecker (1989) for MZP (more details in Fonda Umani and Beran, 2003 and Fonda Umani et al., 2005).

15 Nano- and picoplankton. The assessment of the picoplanktonic and nanoplanktonic fractions was performed according to the Porter and Freig protocol (1980) at the epifluorescence microscope. Aliquots of each sample were stained with a DAPI (4', 6-diamidino-2-phenylindole) solution, $1 \mu\text{g mL}^{-1}$ final concentration and placed in the dark for 15 min. Picoplankton was collected on $0.22 \mu\text{m}$ black polycarbonate filters

20 (Nucleopore, 25 mm) while nanoplankton on $0.8 \mu\text{m}$ black polycarbonate filters (Nucleopore, 25 mm). The filters were immediately placed on slides between two drops of immersion non fluorescent oil and kept at -20°C in the dark. Counts were made using an epifluorescence microscope at $\times 1000$ final magnification; more than 200 cells were counted for each picoplankton and nanoplankton sample. Picoplanktonic samples were counted in triplicates. For the estimation of biomass, nanoplankton was divided into three dimensional classes: 2–3, 3–5 and 5–10 μm as reported by Christaki et al. (2001).

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Cell abundance data were converted in biomass by applying the following conversion factors: 20 fg C cell⁻¹ for heterotrophic bacteria (Ducklow and Carlson, 1992), 200 fg C cell⁻¹ for *Synechococcus* (Caron et al., 1991). The nanoplanktonic organisms were approximated to spheres (diameter equal to the medium value of the belonging dimensional class) in order to multiply their volume for the conversion factor of 183 fg C μm^{-3} (Caron et al., 1995).

2.4 Chlorophyll *a*

Chlorophyll *a* samples were collected by filtering on board from 1 up to 5 L of sea-water through Whatman GF/F glass-fibre filters (45 mm diameter), the membranes were immediately frozen (-20°C) or stored in liquid nitrogen when available. The pigments extraction was run overnight in the dark at 4°C with 90 % acetone from the filter previously homogenized; concentrations were determined with the spectrofluorometer Perkin Elmer LS 50B (450 nm excitation and 665 nm emission wavelengths) measuring the chlorophyll *a* before and after acidification with 2 drops of HCl 1 N (Lorenzen and Jeffrey, 1980). The instrument calibration was made using pure Sigma chl *a* standards and computing a linear response for the considered range.

2.5 Statistics

We calculated the normalised forage ratio (NFR) following Paloheimo (1979) to evaluate the relative selectivity of different food types: $\text{NFR}_i = (r_i/p_i)/\sum(r_i/p_i)$, where r_i represents the biomass percentage of the food type *i* in the consumers diet and p_i is the percentage of that food type in the total available food spectrum.

3 Results

Figure 2 shows the biomass of all primary producers at the surface assessed per each sampling event. Ordination of data per increasing values highlighted three major clus-

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ters with significant differences among them (one-way ANOVA was highly significant, $F = 17.65$, $df = 10.04$, p value < 0.001). They divided the trophic conditions of the sampling events in three distinct clusters: the first one with values for total autotrophic fraction ranging from 0.45 to $6.44 \mu\text{g CL}^{-1}$ that we consider representative of oligotrophic conditions (mean chl *a* 0.22 mg L^{-1}); the second one that we consider mesotrophic with an autotrophic total carbon from 15.32 to $61.93 \mu\text{g CL}^{-1}$ and mean chl *a* of 0.60 mg L^{-1} and the last one which can be considered eutrophic (130.74 – $1104.4 \mu\text{g CL}^{-1}$ and mean chl *a* of 2.60 mg L^{-1}).

The organisms considered in this study were: micro-zooplankton (MZP), micro-phytoplankton (MPP), nano-plankton (NP), heterotrophic picoplankton (HP) and autotrophic picoplankton (AP). The analysed communities in oligotrophic conditions were mostly characterized by the presence of nanoplankton (NP) and heterotrophic picoplankton (HP) whose biomasses represented on average 27.4 and 46.8 % of total biomass, respectively. In mesotrophic conditions MPP for 28.8 %, HP for 33.7 % and AP for 21.1 % almost equally composed the mean total biomass. MPP dominated in eutrophic conditions reaching 91.1 % of the total biomass.

Considering only preys' biomass, in oligotrophic and mesotrophic conditions NP and picoplankton constituted on average almost 80 % of total biomass and picoplankton alone more than 60 %. MPP represented only a small fraction of this biomass and mainly because of the presence of small flagellates. In eutrophic condition, MPP accounted from 78 to 98 % of total preys' biomass and it was principally constituted by diatoms.

When the biomass of the preys increased the equitability (computed with Jaccard index) of MZP major taxa decreased and few species became dominant: in 4 cases they were non-loricate ciliates, in 2 cases Tintinnids (*Stenosemella ventricosa* and *S. nivalis*) and in 1 case another species of protists.

The overview of MZP ingestion rates per each dilution experiment highlights as the daily amount of carbon ingested increased according to the trophic level (Fig. 3). In oligotrophic conditions NP and HP manly supported MZP whose ingestion rates ranged

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from 1.61 to 23.45 $\mu\text{g CL}^{-1} \text{d}^{-1}$ and from 1.80 and 23.84 $\mu\text{g CL}^{-1} \text{d}^{-1}$, respectively. In mesotrophic situations the picoplankton suffered the highest mortality rates with an average of 32.35 $\mu\text{g CL}^{-1} \text{d}^{-1}$ for HP and 9.23 $\mu\text{g CL}^{-1} \text{d}^{-1}$ for AP. MZP ingestion on NP was detected in 7 cases out of 11 and ranged from 1.50 to 8.23 $\mu\text{g CL}^{-1} \text{d}^{-1}$ while MPP ingestion occurred within a range from 1.46 to 23.49 $\mu\text{g CL}^{-1} \text{d}^{-1}$. In eutrophic conditions grazing rates on MPP were the highest ones ranging from 50.97 to 155.19 $\mu\text{g CL}^{-1} \text{d}^{-1}$ followed by ratios on HP (2.25–66.90 $\mu\text{g CL}^{-1} \text{d}^{-1}$), NP (1.08–13.50 $\mu\text{g CL}^{-1} \text{d}^{-1}$) and AP (0.01–5.58 $\mu\text{g CL}^{-1} \text{d}^{-1}$).

By normalizing the ingestion rates on the corresponding prey biomass, the differences among MZP grazing pressure on different prey classes were less evident. In oligotrophic conditions we observed higher grazing efficiency per available biomass on MPP, NP and AP while the highest grazing efficiency for HP occurred in mesotrophic conditions.

HNF ingestion rates among analysed dilution experiments (Fig. 4) indicated as ingestion rates increased with prey availability from oligotrophic to mesotrophic conditions while values decreased in eutrophic conditions. HP represented always the most exploited class of preys with mean ingestion rates of 5.30, 23.41 and 14.80 $\mu\text{g CL}^{-1} \text{d}^{-1}$ respectively; for AP ingestion rates on average ranged from 1.87 $\mu\text{g CL}^{-1} \text{d}^{-1}$ in oligotrophic state to 9.69 $\mu\text{g CL}^{-1} \text{d}^{-1}$ in mesotrophic and 0.36 $\mu\text{g CL}^{-1} \text{d}^{-1}$ in eutrophic conditions.

Normalizing ingestion rates of HNF on the corresponding prey biomass, grazing efficiency on HP available biomass did not show any significant variation among trophic conditions although the highest efficiency occurred in mesotrophic conditions while AP stocks were more heavily exploited in oligotrophic conditions.

MZP ingestion rates increased with the availability of prey biomasses. Data might suggest a sigmoidal trend for the ingestion kinetics with critical values of biomass at which the ingestion rates remain at the minimum and saturation thresholds at which grazing ability of MZP cannot cope with prey biomass increments.

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MZP grazing kinetics (Fig. 5a): on MPP it is possible to hypothesize a critical threshold at $20 \mu\text{g CL}^{-1}$ and a saturation threshold at $250 \mu\text{g CL}^{-1}$ ($r = 0.98$), on NP the critical threshold can be identified at $3 \mu\text{g CL}^{-1}$ and the saturation threshold at $10 \mu\text{g CL}^{-1}$ ($r = 0.71$), on HP a critical threshold at $7 \mu\text{g CL}^{-1}$ and a saturation threshold at $32 \mu\text{g CL}^{-1}$ ($r = 0.78$), for AP the critical threshold seems lower than $2 \mu\text{g CL}^{-1}$ and no saturation threshold was reached ($r = 0.93$).

Grazing kinetics for HNF (Fig. 5b): on HP the critical threshold was lower than $3 \mu\text{g CL}^{-1}$ and saturation threshold set at $35 \mu\text{g CL}^{-1}$ ($r = 0.91$), on AP the critical threshold appeared at $2 \mu\text{g CL}^{-1}$ and again no saturation threshold was reached.

Comparison between potential production (PP) and ingestion (/) rates for the MZP-dilution experiments are reported in Fig. 6a. Data points represent the sum of the mean values of PP and / for each prey classes. In oligotrophic and mesotrophic conditions the ingestion rates mostly overcome the potential productions; in oligotrophy few exceptions were encountered when PP was slightly higher than / due to HP production (31 % of the experiments) while in mesotrophy it was due to HP and MPP productions (36 % of the experiments). In eutrophic conditions PP tends to be higher than / (57 % of the experiments) with the production mainly dependent on the production of AP, HP and partially on the production of MPP.

For HNF-dilution experiments in oligotrophic conditions / rates were higher than PP in 71 % of the cases, with exception at low PP values; in mesotrophic conditions / rates overcame PP in half of the experiments except when PP reached the highest values; in eutrophic conditions the determined PP values were lower than in mesotrophy, however the production tended to overcome / rates in 86 % of the experiments. HP gave a higher contribution than AP to total preys' PP in oligotrophic and eutrophic conditions while AP contribution was higher in mesotrophic conditions.

Results of the normalised forage ratio (NFR) highlighted (Fig. 7) as the relative selectivity of MZP was higher for HP among the three encountered trophic conditions, AP NFR values inversely decreased with the chlorophyll *a* trend while MPP selection in-

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creased from oligotrophic to eutrophic situations. NP were more selected in oligotrophic and eutrophic conditions.

Figure 8a reports HP biomasses estimated for the dilution experiments carried out in the meso- and bathypelagic layers where HP represented the only available prey for HNF. Biomasses generally varied from 0.14 to 0.97 $\mu\text{g CL}^{-1}$ with the exception of two mesopelagic stations with relatively high values of 6.45 $\mu\text{g CL}^{-1}$ and 7.24 $\mu\text{g CL}^{-1}$. The mean biomass for the HNF was 0.37 $\mu\text{g CL}^{-1}$ with a SD of $\pm 0.31 \mu\text{g CL}^{-1}$, and it did not increase where high prey biomass were encountered.

HNF ingestion rates increased with the availability of HP biomass, the kinetics curve (Fig. 8b) underlines a very low critical threshold ($< 0.5 \mu\text{g CL}^{-1}$) and no saturation threshold was evident. The highest ingestion rates were recorded in correspondence of the stations with the highest HP biomasses, however the distribution of the normalized ingestion values did not follow the ingestion trend (Fig. 8c); normalized ingestion reached the highest values at the stations with lower HP biomass.

The relationship between PP and / rates highlighted as when low values of production were measured (between 0.14 and 2.28 $\mu\text{g CL}^{-1} \text{d}^{-1}$) PP was overcame by / values, while when higher values of PP were determined / values overcame the production (data not shown).

Mean values of biomasses and ingestion rates of all considered organisms were used to produce models of trophic carbon pathways for the three trophic conditions described at the surface and in the meso-bathypelagic zones (Fig. 9). In eutrophy, MZP grazed mostly on MPP (mean ingestion 108.42 $\mu\text{g CL}^{-1} \text{d}^{-1}$, mean MPP biomass 326.94 $\mu\text{g CL}^{-1}$) and on HP (mean ingestion 18.24 $\mu\text{g CL}^{-1} \text{d}^{-1}$, mean biomass 17.78 $\mu\text{g CL}^{-1}$) while HNF (here grouped within NP) fed almost uniquely on HP (mean ingestion 14.80 $\mu\text{g CL}^{-1} \text{d}^{-1}$). In this case we can hypothesise that the excess of MPP, not grazed at the surface, can be exported toward the bottom or exploited by larger consumers (mesozooplankton) in a mean amount of 23.07 $\mu\text{g CL}^{-1} \text{d}^{-1}$; it has to be kept in mind that ingestion rates of MZP and HNF were the maximum potential rates for these consumers since they are actively grazed by higher trophic level con-

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sumers in the natural contest. In mesotrophy, MZP principally grazed on HP (mean ingestion $32.35 \mu\text{g CL}^{-1} \text{d}^{-1}$, mean biomass $22.50 \mu\text{g CL}^{-1}$), on MPP and AP ingestion rates were lower (respectively 9.36 and $9.23 \mu\text{g CL}^{-1} \text{d}^{-1}$, on mean biomasses of 19.27 and $14.09 \mu\text{g CL}^{-1}$, respectively). HNF intensely exploited HP ($23.41 \mu\text{g CL}^{-1} \text{d}^{-1}$) and the contribution of AP was also significant ($9.69 \mu\text{g CL}^{-1} \text{d}^{-1}$). In oligotrophy, MZP grazed equally on NP and HP (9.20 and $8.98 \mu\text{g CL}^{-1} \text{d}^{-1}$, on mean biomasses of 4.94 and $8.43 \mu\text{g CL}^{-1}$, respectively). HNF grazed more on HP ($5.30 \mu\text{g CL}^{-1} \text{d}^{-1}$) than on AP ($1.87 \mu\text{g CL}^{-1} \text{d}^{-1}$). In the meso- and bathypelagic layers, HNF could graze only on HP with mean ingestion rate of $3.09 \mu\text{g CL}^{-1} \text{d}^{-1}$ on a mean biomass of $1.33 \mu\text{g CL}^{-1}$.

10 4 Discussion

Data analysed in this study highlighted as MZP fed on a broad range of different preys composed by MPP, NP (autotrophic, heterotrophic and mixotrophic nanoplankton), HP and AP. The heterotrophic fraction of NP, here called HNF, displayed as well an intense grazing activity that affected both the considered classes of picoplankton.

15 MZP and HNF were able to exploit wide ranges of available biomasses as shown by kinetic curves and their trends were similar for shared prey stocks (HP and AP) with few differences: HNF had lower critical values for HP and they were more efficient than MZP to exploit HP biomass even when it was scarce. MZP had higher saturation thresholds for HP and consequently they were able to ingest higher amount of biomass, 20 however none of the consumers reached a saturation threshold for AP.

Overall, the ingestion rates shown a discrete variability among the considered prey stocks and different ecosystems; however the investigated prey classes were not equally affected by grazing pressure. By comparing MZP and HNF ingestion rates on picoplankton it is evident that larger consumers in $> 66\%$ of the analysed dilution experiments had a higher impact in respect to HNF on prokaryotic communities. This result can be interpreted as an evidence for a direct impact of MZP on HP and not only through HNF ingestion (Fonda Umani and Beran, 2003).

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Regarding preys, ingestion rates differently affected each class in the analysed dilution experiments and significant variations were found among the different trophic conditions. In eutrophic condition, the highest mean ingestion rate among preys was detected on MPP that represented more than 80 % of the MZP mean daily diet. Smaller preys as NP and AP presented small contributions to the diet of these consumers although the grazing pressure affecting HP stock was not negligible since they cover almost 14 % of MZP diet. HNF diet, although composed essentially of picoplankton, was for 97.6 % targeted on HP, the prokaryotic fraction offering the highest available biomass. Prokaryotes emerged as performing a key role within the pelagic marine food webs in the examined areas of the Mediterranean Sea characterized by meso- and oligotrophic conditions. For HNF, HP represented > 70 % of their daily diet and the related amount of ingested biomass was just slightly lower than the HP biomass handled by MZP. The contribute of picoplankton in the MZP diet, aspect that is seldom investigated, was noticeable particularly in mesotrophy and oligotrophy where HP resulted the most affected stock. Ingestion rates on HP were higher than on MPP, NP and AP; solely in few experiments NP and AP contributions to MZP diet were higher than the HP one.

The importance of HP in the MZP diet were remarked by the output of NFR index: the normalized forage ratio for these preys were the highest in all trophic conditions representing around 40 % of MZP choices in eutrophic and oligotrophic conditions and almost 60 % in mesotrophic conditions.

By comparing the ingestion rates with the related available biomass of each prey it was shown as the highest values of ingestion occurred when biomasses were higher. High ingestion rates on the picoplankton in meso- and oligotrophy and on MPP in eutrophy can thus be linked with the availability of their biomasses and in turn with their ability to grow in these trophic environmental conditions.

In the eutrophic communities, the high nutrient concentration favoured large MPP cells (able to grow better than picoplankton when relaxed by nutrient depletion, Agawin et al., 2000) leading to outbreaks of diatoms. MPP dominated in eutrophic condi-

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tion: as average they represented 86 % of the total biomass and > 88 % of total prey biomass; as average HP contributed for 8.2 % of the total biomass and 8.4 % of total prey biomass while NP and AP biomasses were very low.

Mesotrophic communities were equally composed by MPP, HP and AP while studied areas characterized by oligotrophy presented communities mostly composed by the smallest plankton: HP and AP that represented on average > 55 % of total biomass (in accordance with findings of Agawin et al., 2000), > 60 % of total prey biomass and respectively 53.4 and 76.2 % of MZP diet. Low nutrient environments are known to favour picoplanktonic organisms: the autotrophic fraction is able to outcompete larger phytoplanktonic cells in the uptakes of inorganic nutrients while the heterotrophic fraction can proficiently exploit bulks of dissolved organic matter.

The overall trend of total ingestion rates for each dilution experiment shown as the amount of prey biomasses ingested by consumers increased according with the trophic state of the ecosystem. Thus eutrophic conditions were characterized by higher carbon fluxes from preys to MZP while the amount of carbon transferred to the upper trophic levels of the marine pelagic food webs decreased in mesotrophic and were minimum in oligotrophic conditions.

However, when the efficiency of the grazing process were investigated (normalizing the ingestion values per the available biomass) it was underlined as at increasing trophic conditions of the system the efficiency of grazing processes decreased, especially for HNF whose values halve. For MZP, normalized values indicate as HP were the most efficiently biomasses exploited (only in oligotrophy NP had comparable values) and the highest efficiency was observed in mesotrophy.

In oligotrophic conditions the normalized ingestion rates of the MZP per single prey class shown values > 1 that suggests high daily turnover ratios for MPP, NP and HP. This state occurred also in mesotrophic and eutrophic conditions but only for HP. HNF never reached normalized ingestion values > 1 except in oligotrophy for the HP; grazing efficiency on HP was always higher than on AP and the efficiency on AP suffered

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a huge decrement from oligotrophic to eutrophic conditions, where it was reduced of almost 70 %.

Grazing efficiency of the consumers can be expressed by the PP-/ balance. This comparison, with some precautions as suggested by Caceres et al. (2013), could be 5 a proxy for the carbon balance of the system thus suggesting the carrying capacity for higher trophic levels. / rates of MZP were averagely higher than the related PP of preys that were efficiently top-down controlled in oligotrophic and mesotrophic conditions, while in eutrophic conditions PP in most of the cases overcome the ingestion. MZP reached the saturation threshold in the kinetic curves and we might hypothesise an 10 export of biomass from primary producers that can sink or be transferred up to higher trophic levels. HNF were not able to exert always an efficient top down control on the picoplanktonic preys in oligotrophic and mesotrophic areas, while in eutrophic areas there was no top-down control at all.

In the meso- and bathypelagic layers biomasses of MZP, HNF and HP were as 15 average > 80 % lower than at the surface, in accordance with Nagata et al. (2000) and Parada et al. (2007); only at two mesopelagic stations HP biomasses were comparable with those at the surface, although the biomass of HNF did not parallel this increase.

Due to the rarefaction of the considered communities we can hypothesise a very limited or any grazing activity of MZP on HP, although MZP grazing effort has never 20 been determined. Also HNF suffer the reduction of prey density and the measured ingestion rates decreased of 73.6 % in respect to surface values; the kinetic curve did not suggest any saturation threshold. Our results suggest that these organisms could adapt to the scarce prey stock and may evolved feeding strategy to exploit very low prey concentration since the critical threshold was lower than $0.5 \mu\text{g CL}^{-1}$.

25 Normalized ingestion rates revealed how the highest efficiency was founded again among stations with lower prey biomasses.

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5 Conclusion

In conclusion, from this wide dataset of dilution experiments the most relevant result is that HP biomasses represented the key source of organic carbon among pelagic food webs in the Mediterranean Sea and that MZP are the principal transfers of biomass toward the upper trophic levels. These consumers, together with HNF, grazed on HP stocks with ingestion rates and efficiency that differed according to the trophic condition encountered. We are well conscious that measured mortality on the considered prey classes might include the viral impact that were not independently assessed nor investigated in the dilution experiments here presented. Several authors quantify the viral impact on prokaryotic communities (Tijdens et al., 2008; Weitz et al., 2015), nevertheless protists represented almost always the main cause of mortality at the surface especially for HP (Domaizon et al., 2003; Di Poi et al., 2013; Chiang et al., 2014; Tsai et al., 2015) while in some cases viral lysis controlled AP populations (Personnic et al., 2009; Weitz et al., 2015). At the meso- and bathypelagic layers, rarefied microorganism communities could suggest that HNF are the principal (and maybe unique) channels of prokaryotic organic matter toward the higher levels of the pelagic food web. Up to now, in the best of our knowledge, grazing experiments on larger consumers were not yet been made in the deep ocean. Therefore considering the scarce presence of MZP, a very simplified food web mostly related to the hot spot theory of Azam and Malfatti (2007) could depicted where HNF alone can exploit the HP biomasses. Viral control of picoplankton communities were also discouraged by Parada et al. (2007) that suggested as “deep-water prokaryotes are apparently far less controlled in their abundance and taxon richness by lytic prokaryotic phages than the high viral abundance and the virus-to-picoplankton ratio would suggest”. Fixed and generalized models of trophic food webs are not reliable because of the intrinsic nature of a food web (prey-predator interaction is one of the major drivers of communities shift); other sources of variability, as nutrients availability, currents or physical events (advection, up- downwelling, runoff), viral lysis and allochthonous stress (e.g.

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pollutants) can shape the trophic food web mutating ratios among the carbon budget sources or sinks.

We are aware of the limit of dilution experiments because they cannot fully represent natural conditions, however they can be used to compare different trophic situations 5 when, as in our case, they are set up following the same protocol. Thus here we proposed some constrains based on the trophic condition of the environment that oriented the carbon flux of the different ecosystems:

10 – In eutrophic conditions where rich available MPP biomasses support high MZP ingestion rates, herbivory is the main trophic pathway. However also in these eutrophic conditions picoplankton, principally HP, represents anyway a not negligible source of carbon. MZP biomass mostly relayed on the MPP however predators were not able to control prey's production thus a likely export can be inferred.

15 – Bacterivory was the major pathway of organic carbon in oligotrophic and mesotrophic environments as well as in the meso- and bathypelagic layers. In mesotrophic conditions MZP mainly grazed on HP while MPP represented only a small part of the diet comparable with the contribution of AP. In oligotrophic conditions MZP based their diet on HP and on NP, MPP represented only a negligible fraction of the total ingestion. At the meso- and bathypelagic levels, HNF relayed only on HP with exploiting efficiency higher than those exerted at the surface.

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Table A1. Sampling sites for surface experiments (at -5 m). Experiments were carried out separately for MZP and HNF. Coordinates are reported according to Decimal Degrees (DD) system.

Cruise	Station	Sampling date	Long (E)	Lat (N)	Depth (m)	Location
OBAMA	CF_16	02 Apr 2011	18.181	39.286	1035	Northern Ionian Sea
OBAMA	MS_03A	01 Apr 2011	18.320	39.330	775	Northern Ionian Sea
OBAMA	O_36	26 Mar 2011	17.267	41.380	1132	Southern Adriatic Sea
OBAMA	O_37B	27 Mar 2011	17.336	41.430	1108	Southern Adriatic Sea
VECTOR	V1	06 Jun 2007	8.000	43.500	2490	Ligurian Sea
VECTOR	V10	22 Jun 2007	28.323	35.953	3870	Aegean Sea
VECTOR	V2	08 Jun 2007	12.999	39.500	3570	Tyrrhenian Sea
VECTOR	V3	05 Jun 2007	6.073	39.314	2850	Sardino-Balearic Sea
VECTOR	V4	01 Jun 2007	-0.998	36.502	2640	Alboran Sea
VECTOR	V6	14 Jun 2007	18.000	38.495	3000	Ionian Sea
VECTOR	V7	16 Jun 2007	20.875	35.135	3200	Aegean Sea
VECTOR	VA	30 May 2007	-8.332	35.000	2776	Atlantic Ocean
VECTOR	VIERA	24 Jun 2007	26.087	34.412	4760	Aegean Sea
Survey	C1	17 Nov 1998	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	08 Feb 1999	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	12 May 1999	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	18 Aug 1999	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	15 Dec 1999	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	07 Feb 2000	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	15 May 2000	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	07 Aug 2000	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	20 Nov 2000	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	12 Feb 2001	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	07 May 2001	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	07 Aug 2001	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	15 Nov 2001	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	13 Feb 2002	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	14 May 2002	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	07 Aug 2002	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	12 Mar 2003	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	29 Sep 2003	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	10 Mar 2004	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	05 Apr 2004	13.710	45.701	17	Northern Adriatic Sea
Survey	C1	09 Aug 2005	13.710	45.701	17	Northern Adriatic Sea

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Table A2. Sampling sites for meso- and bathypelagic experiments (at +5 m from bottom depth). Experiments were carried out only on HNF. Coordinates are reported according to Decimal Degrees (DD) system.

Cruise	Station	Sampling date	Long (E)	Lat (N)	Depth (m)	Location
OBAMA	CF_16	26 Mar 2011	18.181	39.286	1035	Northern Ionian Sea
OBAMA	MS_03A	27 Mar 2011	18.320	39.330	775	Northern Ionian Sea
OBAMA	O_36	02 Apr 2011	17.267	41.380	1132	Southern Adriatic Sea
OBAMA	O_37B	01 Apr 2011	17.336	41.430	1108	Southern Adriatic Sea
OBAMA	OL_107	03 Apr 2011	18.810	39.741	674	Otranto Channel
VECTOR	V1	30 May 2007	8.000	43.500	2490	Ligurian Sea
VECTOR	V10	01 Jun 2007	28.323	35.953	3870	Aegean Sea
VECTOR	V2	05 Jun 2007	12.999	39.500	3570	Tyrrhenian Sea
VECTOR	V3	06 Jun 2007	6.073	39.314	2850	Sardino-Balearic Sea
VECTOR	V4	08 Jun 2007	-0.998	36.502	2640	Alboran Sea
VECTOR	V6	14 Jun 2007	18.000	38.495	3000	Ionian Sea
VECTOR	V7	16 Jun 2007	20.875	35.135	3200	Aegean Sea
VECTOR	VA	24 Jun 2007	-8.332	35.000	2776	Atlantic Ocean
VECTOR	VIERA	22 Jun 2007	26.087	34.412	4760	Aegean Sea

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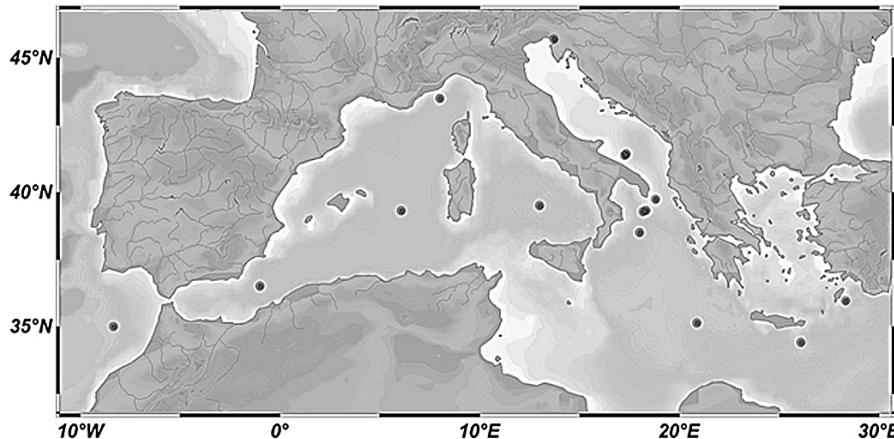


Figure 1. Map of the Mediterranean Sea. The sampling sites are located by the blue dots.

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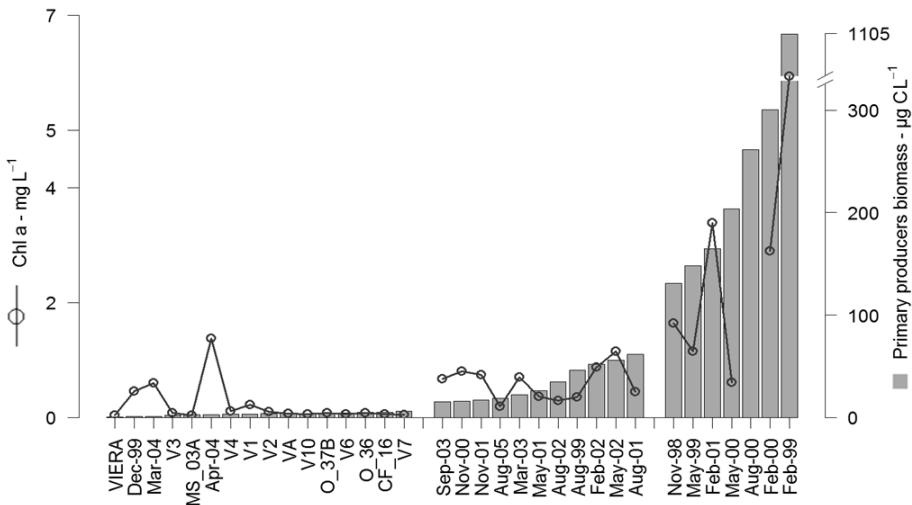


Figure 2. Primary producers' biomass and chlorophyll *a* distribution among sampling events.

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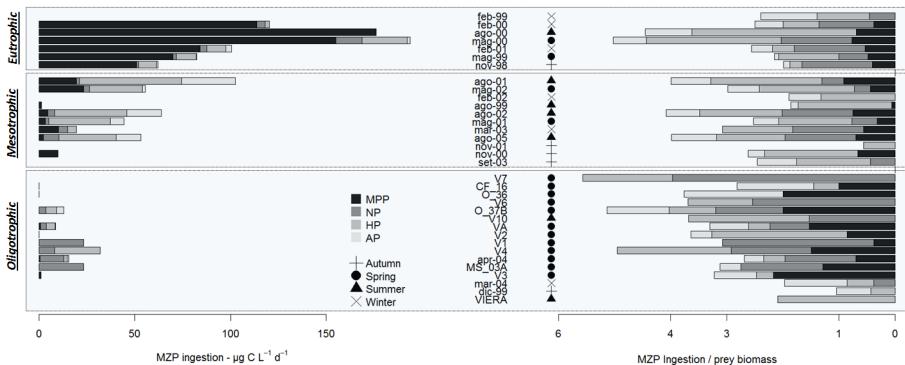


Figure 3. Ingestion rates of MZP among dilution experiments on the left side. Ingestion rates normalized on available biomass on the right side.

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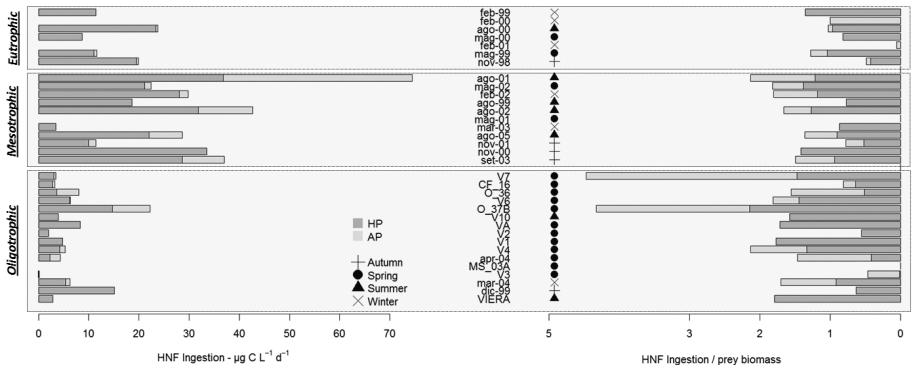


Figure 4. Ingestion rates of HNF among dilution experiments on the left side. Ingestion rates normalized on available biomass on the right side.

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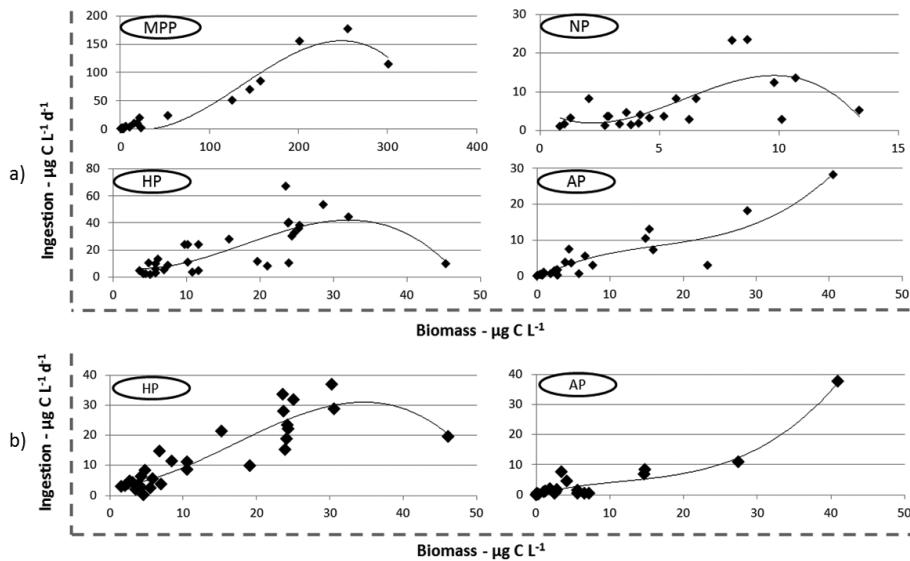


Figure 5. Comparison of ingestion rates of MZP with MPP, NP, HP and AP biomasses (a). Comparison of ingestion rates of HNF with HP and AP biomasses (b).

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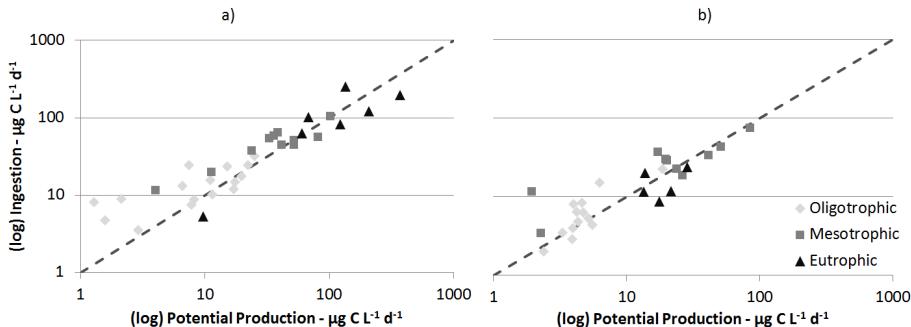
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Figure 6. log-log graph reporting the mean values of all prey classes' potential production vs. MZP ingestion rates for MZP-targeted dilution experiments **(a)** and HNF ingestion rates against prey potential production for HNF-targeted dilution experiments **(b)**. Dashed lines represent graph bisector and thus the equilibrium between / and PP.

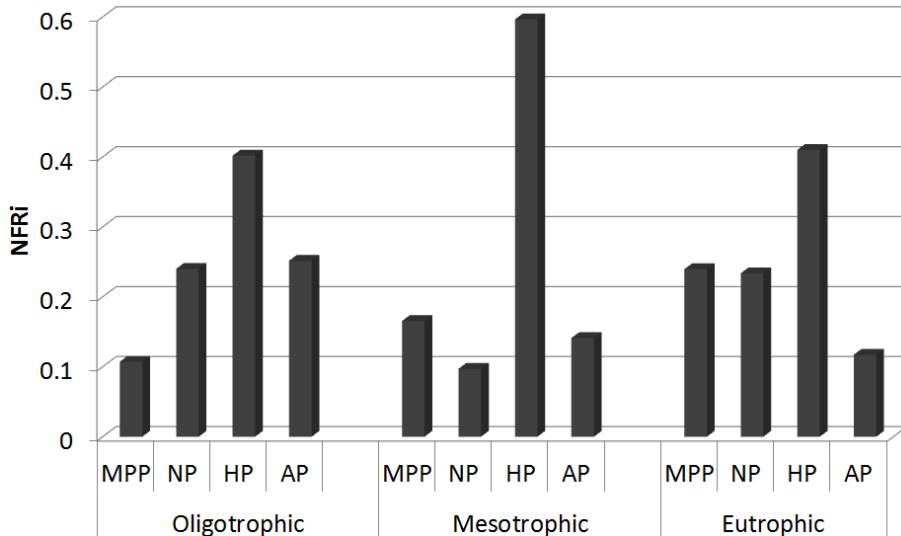
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Figure 7. Mean NFR index estimated for all prey classes of the MZP in the three considered trophic conditions.

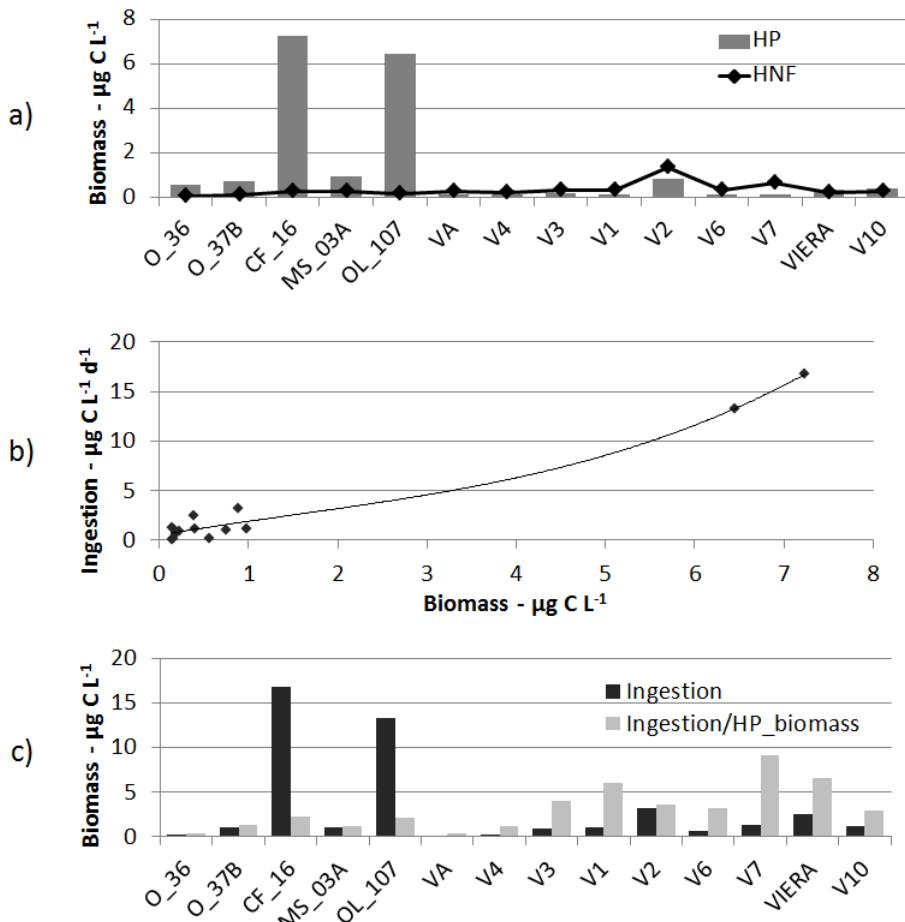


Figure 8. (a) HP biomass for all dilution experiments carried out in the meso- and bathypelagic layers compared to HNF biomass. (b) Ingestion over prey biomasses among the experiments. (c) Comparison of ingestion rates with normalized ingestion rates for all experiments.

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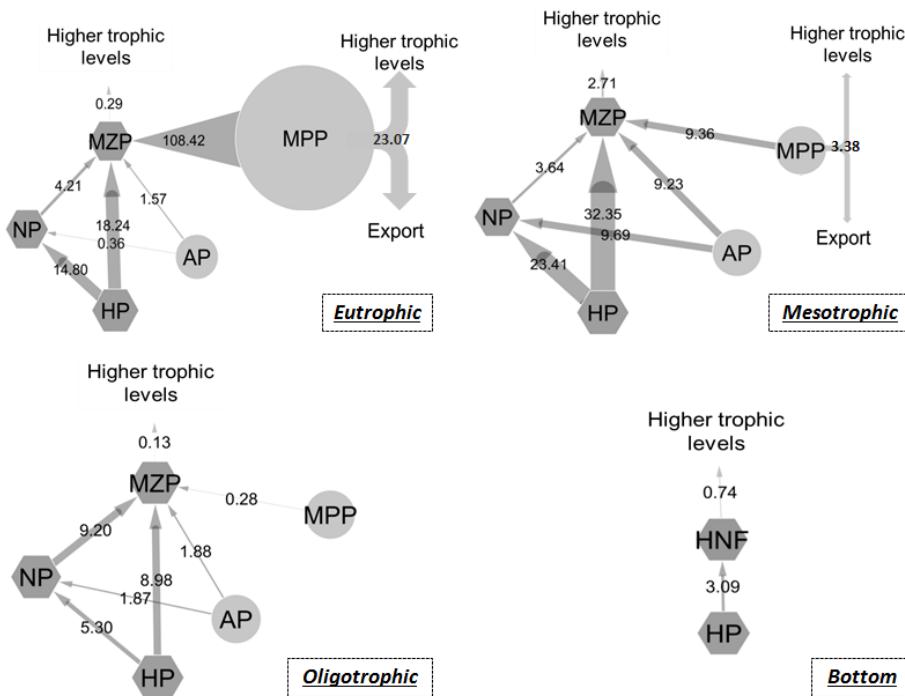


Figure 9. Carbon flux models with mean ingestion rates of MZP and HNF (express as $\mu\text{g C L}^{-1} \text{d}^{-1}$) on considered prey stocks computed at the surface in eutrophic, mesotrophic and oligotrophic conditions and at the mesopelagic and bathypelagic layers only for HNF.

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