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Functional response to food limitation can reduce the impact of global change in the deep-sea benthos

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Abstract

Aim: A key paradigm of deep-sea ecology is that the ocean interior is a food-limited environment, which limits the faunal growth. Here, we estimated the efficiency of deep-sea fauna in exploiting resources to assess the potential response of deep-sea organisms to changes in the food inputs expected with global change.

Location: Mediterranean Sea.

Time period: 1989–2010.

Major taxa studied: Viruses, prokaryotes, meiofauna, macrofauna and megafauna.

Methods: Using the largest data set spanning from microbes to megafauna produced synoptically so far, we investigated patterns of abundance, biomass and ecosystem efficiency across depth-related and longitudinal gradients of food availability in both Western and Eastern Basins of the Mediterranean Sea.

Results: Our results revealed that prokaryotes dominated benthic biomass at depths > 2,000 m. Contrary to what has been reported at a global scale, meiofaunal biomass decreased with increasing water depth more rapidly than macrofauna and megafauna. Meiofauna showed a significant negative log-linear relationship with increasing water depth in the whole Mediterranean Sea, whereas the other benthic components, from viruses to megafauna, did not decrease significantly, decreased or even increased (e.g., prokaryotes) with increasing water depth. Taking all components together, the efficiency of benthic ecosystems in exploiting organic carbon (OC) inputs increased with increasing depth, in both mesotrophic and ultra-oligotrophic conditions of the deep Mediterranean Sea.

Main conclusions: Changes in ecological efficiency in exploiting the energy available in food-limited conditions suggest that deep-sea ecosystems can show a responsive adaptation to changes in OC inputs from the photic zone. Our results contribute to explaining the high efficiency of resource exploitation by consumers in limited trophic conditions and allow us to hypothesize that the consequences of a potential reduction of food supply in deep-sea ecosystems induced by global changes could be less severe than expected.

KEYWORDS
benthic biota, deep sea, ecosystem efficiency, macrofauna, megafauna, meiofauna, prokaryotes, viruses

1 | INTRODUCTION

Benthic deep-sea ecosystems (beneath 200 m depth) represent the largest biome on our planet, covering > 65% of the Earth's surface and hosting > 95% of the global biosphere (Danovaro, Snelgrove, & Tyler, 2014). Characterizing the functioning and dynamics of deep-sea ecosystems is a central issue in marine ecology and is essential to identify the processes of global carbon and nutrient cycling and the response of deep-sea ecosystems to global change (Danovaro et al., 2017; Rogers, 2015; Woolley et al., 2016; Yasuhara, Doi, Wei, Danovaro, & Myhre, 2016).

Benthic fauna play a pivotal role in sedimentary organic matter diagenesis, nutrient cycling and ecosystem functioning in the deep sea (Brown, Gillooly, Allen, Savage, & West, 2004). The life history, longevity and metabolic rates of deep-sea organisms are influenced by body size and temperature (metabolic theory of ecology; Brown et al., 2004). Deep-sea ecosystems see a progressive (both chemical and thermal) energy limitation with increasing water depth. The inputs of organic material produced by photosynthesis at the ocean surface decrease exponentially with increasing water depth, thus limiting benthic production and controlling the biodiversity of some large species (i.e., Ophiuroidea; McClain, Allen, Tittensor, & Rex, 2012; Smith et al., 2009; Woolley et al., 2016). Such progressive food limitation in the deep sea can have different effects on different benthic components. Recently, McClain et al. (2012) highlighted that the relative influence of chemical (i.e., food) and thermal energy (bottom water temperature) on deep-sea organisms varies considerably across levels of biological organization and that chemical energy has a major effect on larger organisms (at higher levels of biological organization).

Quantitative synoptic information on benthic prokaryotes, meiofauna, macrofauna and megafauna in the deep sea, according to an 'end-to-end' perspective, is extremely limited (Rex et al., 2006; Wei, Rowe, & Escobar-Briones, 2010 and literature therein). A consistent conclusion of these meta-analyses is the decline of benthic abundance and biomass with increasing water depth, particularly evident for macrofauna and megafauna and to a lesser extent for meiofauna (Gambi, Lampadariou, & Danovaro, 2010; Rex et al., 2006; Rogers, 2015; van der Grient & Rogers, 2015; Wei et al., 2010). Investigations carried out on smaller benthic components (e.g., bacteria and protozoa) reveal barely decreasing or invariant bathymetric patterns (Danovaro, Manini, & Dell'Anno, 2002; Deming & Carpenter, 2008; Rex et al., 2006; Wei et al., 2010). The decrease of benthic faunal abundance and biomass with increasing water depth is explained by the exponential decrease in organic matter supply (Jones et al., 2014; McClain et al., 2012), as reported in the Pacific and Atlantic Oceans, where a close relationship between food limitation and decreasing deep-sea standing stocks has been repeatedly observed (Jones et al., 2014; McClain et al., 2012; Smith et al., 2009). An increasing number of studies predict that global change, enhancing water column stratification through increased sea surface temperature, might reduce the input of food resources in some deep-sea regions, such as in the Mediterranean Sea (Coma et al., 2009; Smith, De Leo, Bernardino, Sweetman, & Arbizu, 2008; Sweetman,

Thurber, & Smith, 2017). The effects of global change on food supply to the deep sea might change significantly among different regions and habitats (e.g., northern versus southern hemisphere, or active canyons versus passive open slopes; Cartes, Maynou, Fanelli, López-Pérez, & Papiol, 2015; Pusceddu et al., 2013, 2016; Sweetman et al., 2017). In turn, a reduced food availability can significantly affect the growth rates, survival and recruitments of benthic organisms, with severe consequences on the potential of deep-sea assemblages to sustain their abundance, growth rate, reproduction and recovery of degraded habitats (Barbier et al., 2014; Pusceddu et al., 2014; Smith et al., 2008; Van Dover et al., 2014). However, the potential of deep-sea assemblages to adapt to progressive food depletion is completely unknown. Here, we used the Mediterranean Sea as a model for evaluating the possible effects of changes in food supply [i.e., organic carbon (OC) fluxes] and bioavailability (as quantity of food sources) on the abundance and biomass of different deep-sea benthic components.

We hypothesize that microbes, meiofauna, macrofauna and megafauna will display a different response in terms of abundance and biomass to changes in food sources in regions characterized by different levels of primary productivity (from very low, such as the Eastern Basin, to moderate, such as the Western Basin). To test this hypothesis, we collected the largest synoptic data set produced so far for abundance and standing stock of viruses, prokaryotes, meiofauna, macrofauna and megafauna along bathymetric gradients in different regions of the Mediterranean Sea. We also estimated the changes of benthic biota efficiency in exploiting the food resources at 1,500 and 3,000 m, to assess the potential response of deep-sea organisms to the expected decrease of food availability predicted for several deep-sea regions in the coming decades.

2 | MATERIALS AND METHODS

2.1 | The study area

The deep Mediterranean Sea is divided into the Western and Eastern Basins by the Sicily channel, and the average depth is c. 1,450 m, much shallower than the average depth of the world oceans (c. 4,000 m).

The main features of the deep Mediterranean Sea are as follows: (a) stable homeothermy from c. 300–500 m down to the bottom, with bottom temperatures of c. 12.8–13.5 °C in the Western Basin and 13.5–15.5 °C in the Eastern basin (Emig & Geistdoerfer, 2004); (b) high oxygen concentrations of deeper water masses, such as 210 μmol kg^{-1} in the Western Basin (Tanhua et al., 2013) and 205 μmol kg^{-1} in the Aegean Sea, Eastern Basin (Klein et al., 1999); (c) differences in primary production and thus in organic matter inputs to the seafloor (15–80 times higher in the Western than in the Eastern Basin; Danovaro, Dinet, Duineveld, & Tselepides, 1999; Giordani et al., 2002) and in the benthic trophic state [an eastward decreasing gradient from mesotrophic/oligotrophic (moderate/low organic matter loads) to ultra-oligotrophic (extremely low organic matter loads) conditions; Gambi, Pusceddu, Benedetti-Cecchi, & Danovaro, 2014; Giordani et al., 2002; Pusceddu, Dell'Anno, Fabiano, & Danovaro, 2009; Pusceddu, Gambi, Zeppilli, Bianchelli, & Danovaro, 2009]; (d) lack of major anthropogenic
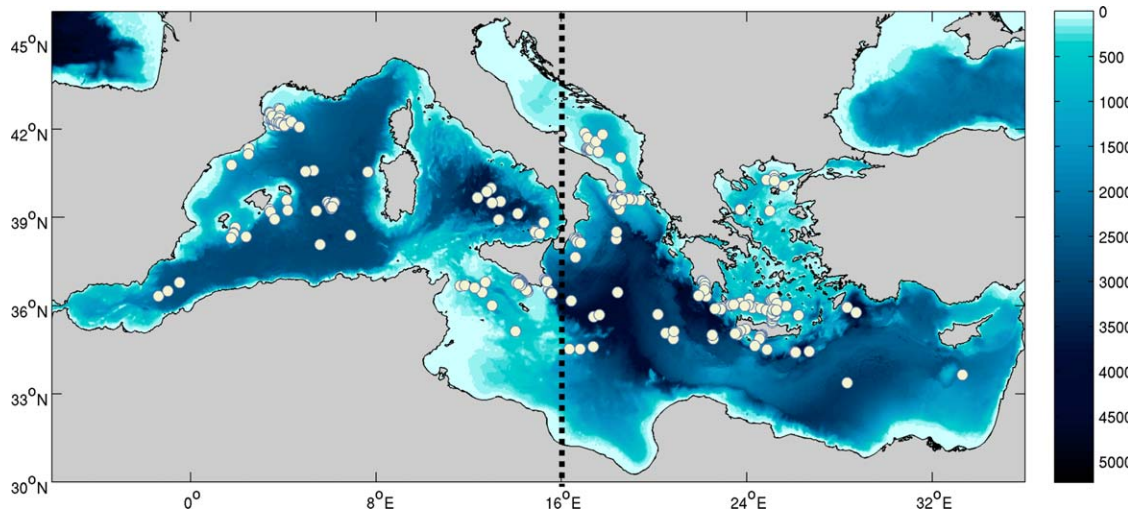
FIGURE 1 Location of the sampling sites in the deep Mediterranean Sea. The vertical dashed line indicates the subdivision of the Western and Eastern Basin. The vertical bar represents the bathymetric ranges (in metres)

contaminations in the deep sea (Danovaro, 2003); and (e) a general decrease of biodiversity with depth, especially for macrofauna and megafauna (Danovaro, Company, & Corinaldesi, 2010).

2.2 | Benthic abundance and biomass

We compiled a cumulative inventory of 1,509 data sets of abundance and biomass from viruses to megafauna (including invertebrates and fishes) obtained from new data and published results within the bathymetric interval 117–4,394 m in the deep Mediterranean Sea (Figure 1; Appendix S1 in Supporting Information).

The abundance and biomass of viruses, prokaryotes and meiofauna were analysed by the same inter-calibrated researchers, using similar sampling devices (oceanic box-corer and multicorer) and the same standardized protocols. Macrofaunal and megafaunal abundance and biomass, instead, were determined by different researchers but using the same methodologies, mesh size and approaches, thus minimizing the possible methodological bias.

The benthic foraminifera were not included in this investigation because of the limited information on this component in the deep Mediterranean Sea and difficulties in estimating their biomass (Rex et al., 2006; Sabbatini, Morigi, Nardelli, & Negri, 2014; Soltwedel, 2000; Wei et al., 2010).

2.3 | Carbon content associated with viral particles and prokaryotic biomass

Benthic viral abundances (expressed as viruses per gram of dry sediment) were determined on 265 samples collected in different sectors of the deep Mediterranean Basin at depths ranging from 183 to 4,347 m. Viral abundances were converted into carbon (C) content assuming conversion factors of 0.06 and 0.08 fg C virus^{-1} (estimated for different benthic deep-sea ecosystems, including the Mediterranean Sea; Dell'Anno, Corinaldesi, & Danovaro, 2015). Such conversion

factors are conservative because they are much lower than those previously assumed for estimating the C content contained in marine viruses (i.e., 0.2 fg C virus^{-1}; Suttle, 2007; Wilhelm & Suttle, 1999).

Benthic prokaryotic abundances (expressed as number of cells per gram of dry sediment) were determined on 508 samples collected in different sectors of the deep Mediterranean Basin at depths ranging from 183 to 4,347 m. Prokaryotic biomass was estimated from prokaryotic biovolume converted to C content assuming 310 fg C μm^{-3} (Danovaro, Dell'Anno, et al., 2008). Viral and prokaryotic abundance and biomass were then normalized to units of sediment surface (i.e., square metres) assuming a sediment density of 1.8 and an average sediment water content of 50% (Dell'Anno & Danovaro, 2005).

2.4 | Meiofauna

Meiofauna included 501 data sets for abundance and biomass, respectively, from the Western to the Eastern Mediterranean Basins at depths ranging from 183 to 4,345 m. Meiofaunal abundance was reported as individuals per square metre. Meiofaunal biomass was obtained from the individual biomass of specimens belonging to the different taxa (Danovaro, 2010). For nematodes, body mass was calculated from the biovolume (V), which was estimated using the Andrassy (1956) formula ($V = L \times W^2 \times 0.063 \times 10^{-5}$, in which body length is L, and the width is W). The biovolumes of all other taxa were derived from measurements of body length (L, in millimetres) and width (W, in millimetres), using the formula $V = L \times W^2 \times C$, where C is the approximate conversion factor for each metazoan meiofaunal taxon (Feller & Warwick, 1988). Each body volume was multiplied by an average density (1.13 g cm^{-3}) to obtain the biomass [in micrograms dry weight (DW)] assuming that the dry : wet weight ratio is 25% and that C content accounts for 40% of the DW (Feller & Warwick, 1988). Data of C biomass measured according to Jensen (1984) were recalculated according to Feller and Warwick (1988). Meiofaunal biomass was reported as grams of carbon per square metre.

2.5 | Macrofauna and megafauna

Macrofaunal and megafaunal abundance and biomass (expressed as individuals per square metre and grams of carbon per square metre, respectively) included 143 and 92 data sets, respectively, and covered different sectors of the deep Mediterranean Sea at depths ranging from 117 to 4,394 m. Macrofaunal organisms were weighed to obtain the biomass value expressed as DW (oven-drying at 60 °C for 24 h). The organic C content was estimated assuming that it represented 35% of the DW. Megafaunal biomass was obtained by converting wet weight into C content using an average value of 7.25%, obtained from the conversion factors reported in the literature for different taxa (Feller & Warwick, 1988; Galéron, Sibuet, Mahaut, & Dinet, 2000; Ricciardi & Bourget, 1998; Rowe, 1983; Soltwedel, 2000).

2.6 | Organic carbon inputs and total phytopigments in deep-sea sediments

Organic carbon fluxes that reach the sea floor through particle sinking were estimated on a decadal time scale from 1998 to 2008 on the basis of the net photosynthetic primary production, which was extracted from the ocean productivity database (www.science.oregonstate.edu/ocean.productivity/index.php) and derived from a C-based productivity model algorithm (Behrenfeld, Boss, Siegel, & Shea, 2005). OC fluxes refer to the same areas investigated for the abundance and biomass of benthic assemblages (Supporting Information Appendix S2). To confirm the general patterns derived from satellite observations, we also considered data of OC fluxes obtained from field measurements (by sediment trap deployments) at selected sites across depth and longitudinal gradients of food availability in the deep Mediterranean Sea (Supporting Information Appendix S2). Data of OC fluxes were collected by sediment traps deployed *c.* 30 m above the seafloor, and average values on a daily basis (in milligrams of carbon per square metre per day) were calculated from OC fluxes collected over a period of 1 year.

As a proxy of freshly deposited material in deep-sea sediments, we used sedimentary contents of total phytopigments, once converted into C equivalents as outlined by Danovaro (2010).

2.7 | Temperature

Data of bottom water temperature (in degrees Celsius) were collected across the Mediterranean Sea from the Western to the Eastern Basin in selected areas investigated for benthic deep-sea biomass. A conductivity–temperature–depth profiler was used to measure bottom water temperature (Danovaro, Molari, Corinaldesi, & Dell'Anno, 2016). Temperature data sources are reported in Supporting Information Appendix S1.

2.8 | Ecosystem efficiency

We estimated the ecosystem efficiency using the following three independent indicators: (a) the ratio of benthic biomass to OC fluxes

(Danovaro, Gambi, et al., 2008); (b) the ratio of benthic biomass to freshly deposited OC (as total phytopigment content in the sediments, converted into C equivalents; Danovaro et al., 2002); and (c) the ratio of benthic biomass to the *in situ* benthic respiration (data from Molari, Manini, & Danovaro, 2013). The ratio of the benthic biomass to OC fluxes and to freshly deposited OC was calculated in selected areas, at 1,500 and 3,000 m depth (megafauna contribution is not available), in the Western and Eastern Basins. The ratio between the biomass and the *in situ* benthic respiration was calculated only at selected sites located at *c.* 3,000 m depth in both basins owing to paucity of information of benthic respiration at shallower depth. The two basins were used as representative of the mesotrophic/oligotrophic (Western Basin) and ultra-oligotrophic (Eastern Basin) conditions of the deep Mediterranean Sea.

2.9 | Data analysis

To examine the relationships between abundance and standing stocks versus depth, maintaining constant latitude and longitude, we used a partial regression analysis according to the approach reported by Rex et al. (2006) and Wei et al. (2010). The multiple regression residuals of abundance and standing stocks against latitude and longitude were used as dependent variables to regress against water depth. To bring the dependent variable back to an appropriate scale, the *y* intercept from the multiple regression was added to the residuals. The same approach was used for the regression analyses of biomass versus temperature and biomass versus OC fluxes, respectively. The fit of the regression models was obtained based on the output of the partial regression analysis.

3 | RESULTS

3.1 | Bathymetric patterns of abundance

Here we find that, among all of the investigated benthic components, only meiofauna show a significant negative log-linear relationship between the abundance and the water depth either consistently in the whole Mediterranean Sea or in the Western and Eastern Basins (Figure 2; Table 1). All other investigated benthic components show different and regionally variable bathymetric patterns. In the Western Mediterranean, the abundance of prokaryotes and megafauna significantly decreases with increasing water depth, whereas that of macrofauna significantly increases, and viral abundance does not change (Figure 2b; Table 1). In the Eastern Basin, all components, except for megafauna, display significant log-linear relationships between abundance and water depth, but these are negative for viruses and macrofauna, and positive for prokaryotes (Figure 2c; Table 1).

3.2 | Bathymetric patterns of biomass

Our results show significant and negative log-linear relationships between the biomass of all components, except for viruses and prokaryotes, and the water depth in the whole Mediterranean Sea (Figure 3a; Table 1). In the Western Basin, only the biomass of prokaryotes and
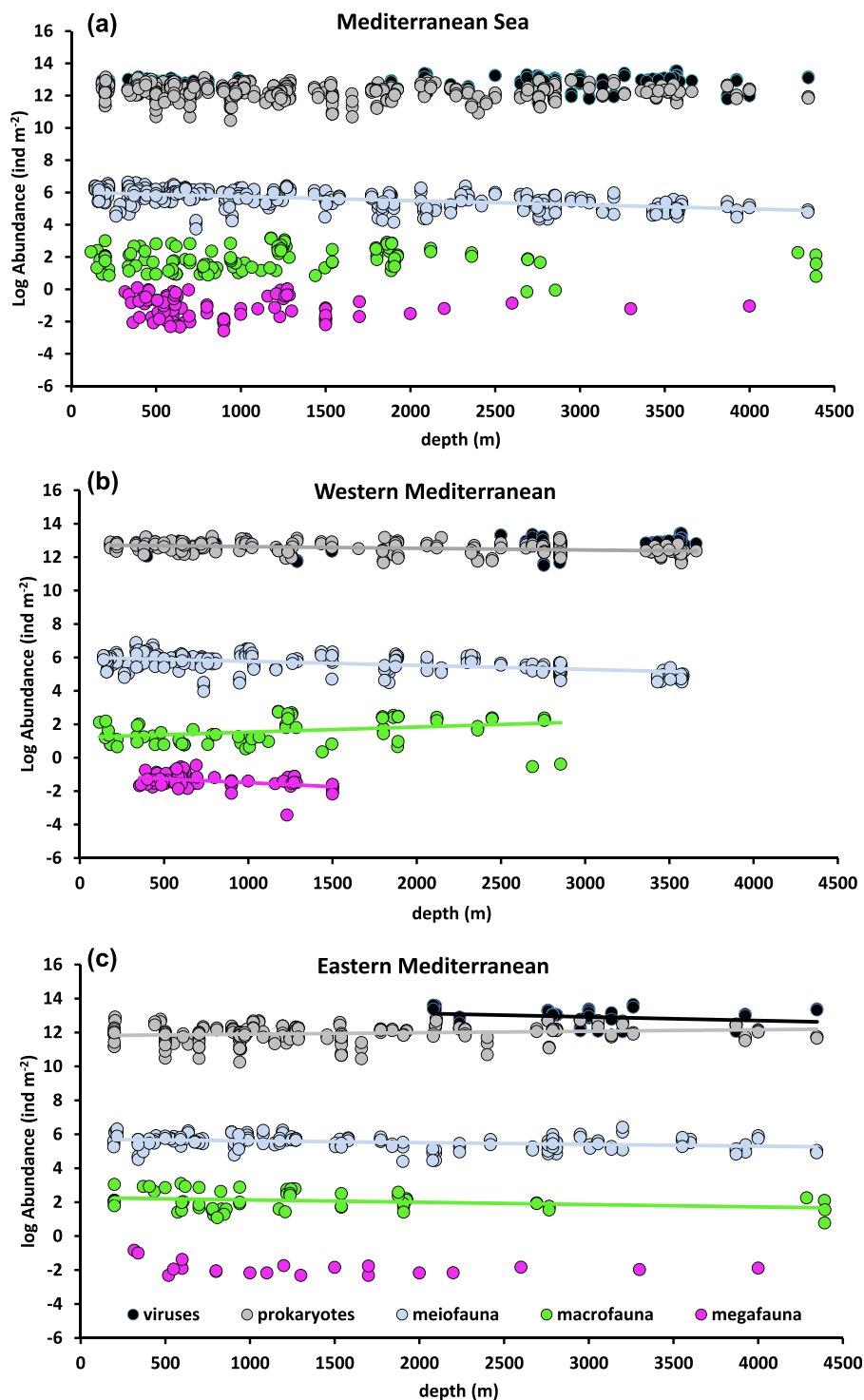
FIGURE 2 Relationships between abundance and depth in the Mediterranean Basin. Reported is the abundance (log$_{10}$-transformed) as a function of depth for viruses, prokaryotes, meiofauna, macrofauna and megafauna (effects of longitude and latitude were removed by partial regression) in (a) the whole Mediterranean Sea, (b) the Western and (c) the Eastern Basin. Only lines of significant relationships are reported (see Table 1)

meiofauna significantly decreases with increasing water depth (Figure 3b; Table 1). In the Eastern Basin, viral, meiofaunal and macrofaunal biomass displays significant negative relationships with water depth, whereas prokaryotic biomass increases along the bathymetric gradient (Figure 3c; Table 1). The analysis of the meiofaunal individual biomass

shows a significant and negative log-linear relationship with the increasing water depth in both Mediterranean Basins (Supporting Information Appendix S3).

The contribution of each benthic component to the total biomass shows that different groups dominate the total biomass at different

TABLE 1 Regression analyses of benthic abundance and biomass against depth for viruses, prokaryotes, meiofauna, macrofauna and megafauna

Regression	Equation	n	R^2	p-value
Log$_{10}$ abundance (individuals m^{-2})				
Whole Mediterranean Sea				
Viruses	$y = -7 \times 10^{-6}x + 12.8$	265	5.5×10^{-4}	n.s.
Prokaryotes	$y = -3 \times 10^{-5}x + 12.3$	508	3.4×10^{-3}	n.s.
Meiofauna	$y = -3 \times 10^{-4}x + 6.0$	501	3.2×10^{-1}	***
Macrofauna	$y = +5 \times 10^{-5}x + 1.8$	143	1.8×10^{-2}	n.s.
Megafauna	$y = -4 \times 10^{-5}x - 1.1$	92	1.3×10^{-3}	n.s.
Western Basin				
Viruses	$y = +3 \times 10^{-4}x + 12.7$	199	1.1×10^{-2}	n.s.
Prokaryotes	$y = -1 \times 10^{-4}x + 12.7$	265	1.0×10^{-1}	***
Meiofauna	$y = -2 \times 10^{-4}x + 6.0$	297	3.2×10^{-1}	***
Macrofauna	$y = +3 \times 10^{-4}x + 1.2$	80	9.5×10^{-2}	***
Megafauna	$y = -5 \times 10^{-4}x - 1.0$	72	1.5×10^{-1}	***
Eastern Basin				
Viruses	$y = -2 \times 10^{-4}x + 13.6$	66	7.1×10^{-2}	*
Prokaryotes	$y = +9 \times 10^{-5}x + 11.8$	243	3.3×10^{-2}	***
Meiofauna	$y = -1 \times 10^{-4}x + 5.7$	204	1.0×10^{-1}	***
Macrofauna	$y = -1 \times 10^{-4}x + 2.3$	63	7.1×10^{-2}	*
Megafauna	$y = -1 \times 10^{-4}x - 1.7$	20	8.0×10^{-2}	n.s.
Log$_{10}$ biomass (gC m^{-2})				
Whole Mediterranean Sea				
Viruses	$y = -1 \times 10^{-17}x - 3.5$	265	5.5×10^{-3}	n.s.
Prokaryotes	$y = -2 \times 10^{-5}x - 1.4$	508	4.0×10^{-4}	n.s.
Meiofauna	$y = -4 \times 10^{-4}x - 0.5$	501	3.4×10^{-1}	***
Macrofauna	$y = -2 \times 10^{-4}x - 0.9$	143	5.8×10^{-2}	**
Megafauna	$y = -2 \times 10^{-4}x - 1.1$	92	6.4×10^{-2}	*
Western Basin				
Viruses	$y = +3 \times 10^{-5}x - 3.6$	199	1.1×10^{-2}	n.s.
Prokaryotes	$y = -1 \times 10^{-4}x - 1.0$	265	1.0×10^{-1}	***
Meiofauna	$y = -3 \times 10^{-4}x - 0.8$	297	3.3×10^{-1}	***
Macrofauna	$y = -1 \times 10^{-4}x - 1.4$	80	9.5×10^{-3}	n.s.
Megafauna	$y = -5 \times 10^{-5}x - 1.6$	72	1.6×10^{-3}	n.s.
Eastern Basin				
Viruses	$y = -2 \times 10^{-4}x - 2.7$	66	7.1×10^{-2}	*
Prokaryotes	$y = +9 \times 10^{-5}x - 1.9$	243	3.4×10^{-2}	**
Meiofauna	$y = -4 \times 10^{-4}x - 0.2$	204	2.1×10^{-1}	***
Macrofauna	$y = -4 \times 10^{-4}x - 0.4$	63	3.0×10^{-1}	***
Megafauna	$y = -2 \times 10^{-4}x - 1.1$	20	1.9×10^{-1}	n.s.

n = number of samples; n.s. = not significant. Note. Response variables are log$_{10}$-transformed; predictor is depth (in metres). Scatter plots of the response variables against predictor and regression lines are in Figures 2 and 3. *$p < .05$. **$p < .01$. ***$p < .001$.
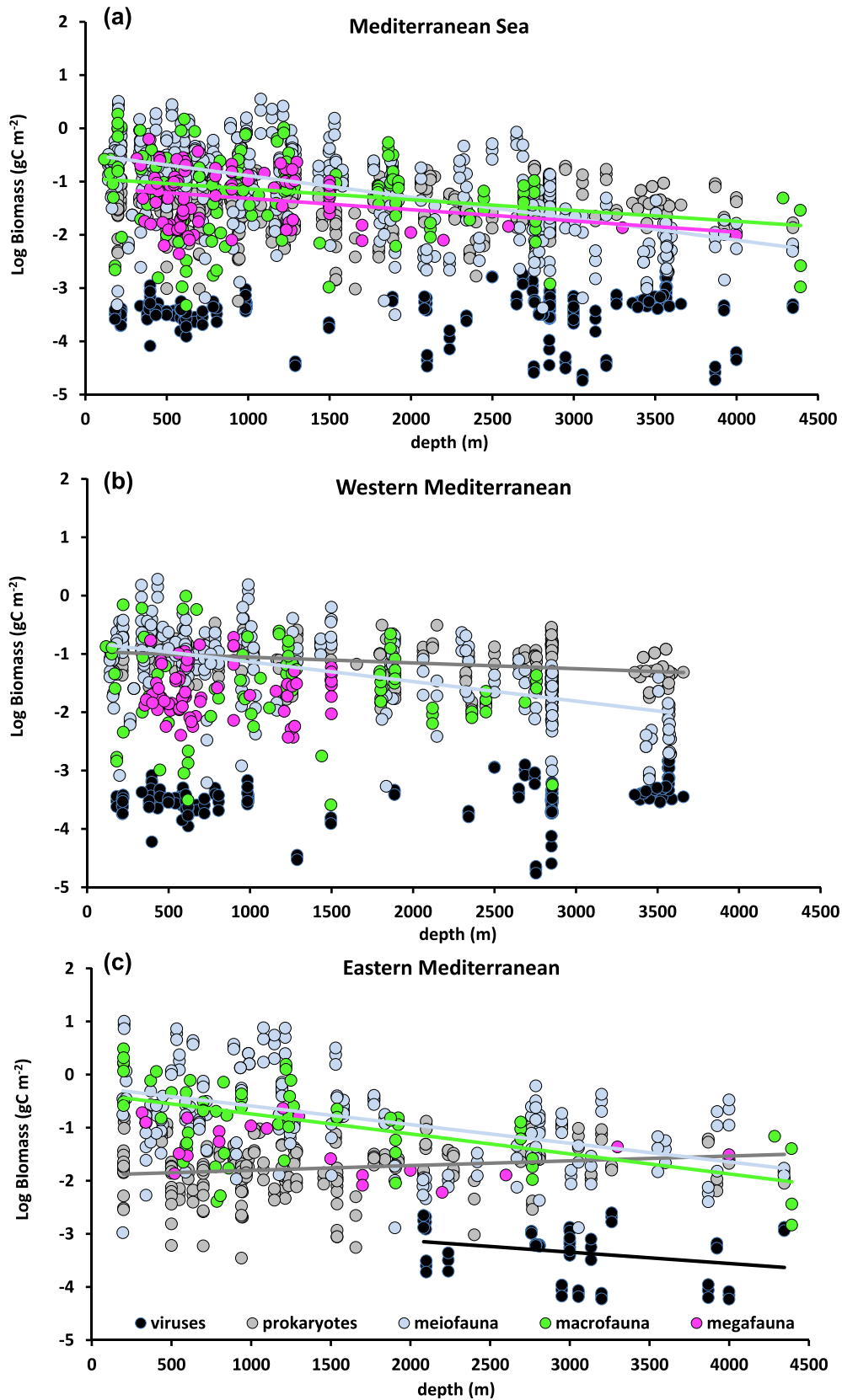
FIGURE 3 Relationships between biomass and depth in the Mediterranean Basin. Reported is the biomass (log_{10}-transformed) as a function of depth for viruses, prokaryotes, meiofauna, macrofauna and megafauna (effects of longitude and latitude were removed by partial regression) in (a) the whole Mediterranean Sea, (b) the Western and (c) the Eastern Basin. Only lines of significant relationships are reported (see Table 1)
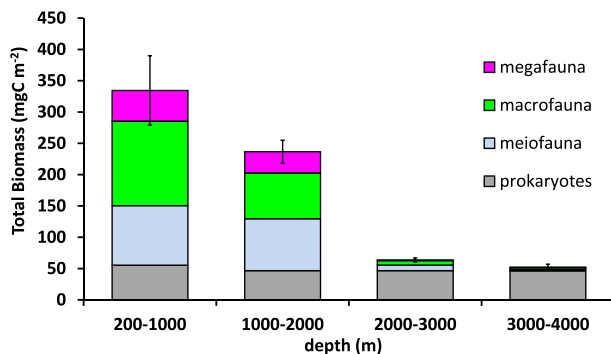
FIGURE 4 Relative contribution of each benthic component to the total biomass estimated for the selected depth intervals. Data of macrofauna in the depth range 3,000–4,000 m are collected at *c.* 4,300 m. Viruses are not shown, and their contribution ranges from 0.1 to 0.8% with the increasing of depth

bathymetric ranges (Figure 4). Macrofauna dominate above 1,000 m depth (*c.* 41% of the total benthic biomass), macrofauna and meiofauna (*c.* 31 and 35%, respectively) co-dominate between 1,000 and 2,000 m depth, whereas prokaryotes (73–88%) become largely dominant below 2,000 m depth. The contribution of viruses to the total benthic biomass is almost negligible at the shallower depth ranges, but *c.* 1% below 3,000 m depth. Overall, the total benthic biomass in the deep Mediterranean Basin (depth range 200–4,000 m) is estimated in *c.* 0.34 Mt C and is largely accounted for by the stock resident in the depth interval between 200 and 1,000 m (*c.* 52%), followed by that in the depth interval between 1,000 and 2,000 m (*c.* 30%) (Supporting Information Appendices S2 and S4).

3.3 | Relationship between benthic biomass and temperature

Our analyses reveal significant positive relationships only between bottom-water temperature and benthic prokaryotic biomass in the Western Basin and with bottom-water temperature and meiofaunal biomass in the whole Mediterranean Sea (Figure 5a,b; Table 2).

3.4 | Relationship between biomass and OC fluxes

Food inputs, estimated in terms of OC fluxes, decrease from the mesotrophic/oligotrophic Western Mediterranean Basin to the ultra-oligotrophic Eastern Basin (Supporting Information Appendix S5). Meiofaunal biomass is positively and significantly correlated with OC fluxes in both basins. A positive relationship is also observed for prokaryotic biomass in the Western Basin and for macrofaunal and megafaunal biomass in the Eastern Basin (Figure 6a,b; Table 2). The rate of increasing biomass with the increasing of OC fluxes is generally steeper for meiofauna than for macrofauna and megafauna, and the rate is generally higher in the ultra-oligotrophic Eastern Basin than in the mesotrophic/oligotrophic Western one (Figure 6a,b).

3.5 | Relationship between benthic biomass and ecosystem efficiency

Ecosystem efficiency, estimated as the ratio of total benthic biomass to OC fluxes, increases with increasing water depth in both investigated regions (Figure 7a). The analysis of ecosystem efficiency, estimated as the ratio of benthic biomass to freshly deposited OC, reveals the same increasing pattern with increasing water depth in the Eastern Basin (Figure 7b). Overall, among the different benthic components investigated, the ecosystem efficiency is primarily dependent on the contribution of prokaryotes (Figure 7c). This pattern is also confirmed when the efficiency is estimated as the ratio between prokaryotic biomass and total phytopigments (data not shown). The higher efficiency of the benthic ecosystem in Eastern Mediterranean Basin is also evident from the ratio between the benthic biomass and respiration (Figure 7d).

4 | DISCUSSION

4.1 | Abundance versus standing stock in the deep Mediterranean Sea

Our investigation reveals that the abundance and biomass of the different benthic components show variable patterns with increasing water depth in the Mediterranean Sea and differ from the patterns observed at global scale (Rex et al., 2006; Wei et al., 2010). Only meiofauna display a consistent significant negative relationship with water depth (for
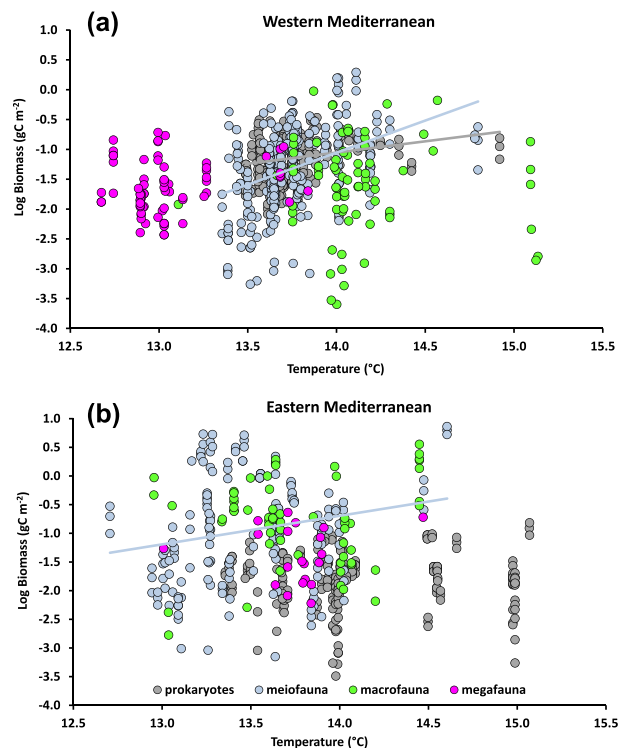

FIGURE 5 Relationship between biomass (log$_{10}$-transformed, in grams of carbon per square metre) and bottom water temperature (in degrees Celsius) in the (a) Western and (b) Eastern Basins of the Mediterranean Sea. Only lines of significant relationships are reported (see Table 2)

TABLE 2 Regression analysis for prokaryotes, meiofauna, macrofauna and megafauna of benthic biomass versus temperature or versus organic carbon fluxes

Regression	Equation	n	R^2	p-value
Temperature				
Western Basin				
Prokaryotes	$y = +0.86x - 14.5$	256	5.5×10^{-2}	***
Meiofauna	$y = +2.47x - 37.0$	288	1.7×10^{-1}	***
Macrofauna	$y = -0.31x + 0.8$	79	3.8×10^{-3}	n.s.
Megafauna	$y = +0.64x - 12.1$	72	3.4×10^{-2}	n.s.
Eastern Basin				
Prokaryotes	$y = -0.02x - 3.9$	234	3.8×10^{-5}	n.s.
Meiofauna	$y = +1.15x - 17.7$	186	4.2×10^{-2}	*
Macrofauna	$y = +0.51x - 8.8$	61	1.4×10^{-2}	n.s.
Megafauna	$y = +0.30x - 7.2$	20	4.7×10^{-3}	n.s.
Organic carbon fluxes				
Western Basin				
Prokaryotes	$y = +0.51x - 1.6$	265	1.1×10^{-1}	***
Meiofauna	$y = +1.31x - 2.5$	297	2.6×10^{-1}	***
Macrofauna	$y = +0.37x - 1.9$	80	8.1×10^{-3}	n.s.
Megafauna	$y = +0.24x - 1.9$	72	5.2×10^{-3}	n.s.
Eastern Basin				
Prokaryotes	$y = -0.29x - 1.6$	234	1.3×10^{-2}	n.s.
Meiofauna	$y = +3.0x - 3.0$	186	2.9×10^{-1}	***
Macrofauna	$y = +2.50x - 2.7$	61	4.5×10^{-1}	***
Megafauna	$y = +2.81x - 3.3$	20	5.2×10^{-1}	***

n = number of samples; n.s. = not significant. *Note.* Response variable is biomass $\log_{10}$-transformed (in grams of carbon per square metre); predictor is temperature (in degrees Celsius) and organic carbon fluxes $\log_{10}$-transformed (in grams of carbon per square metre per year). Scatter plots of the response variables against predictor and regression lines are in Figures 5 and 6. *$p < .05$. ***$p < .001$.

both abundance and biomass), whereas all other benthic components (including viruses and prokaryotes) remain stable, decrease or increase. Moreover, we report here that the decline of meiofaunal biomass with increasing water depth is more evident than the decline of abundance, suggesting that the decrease of food supply to the deep sea can determine a shift of the size of individuals, leading to miniaturization at deeper depths (see the discussion below).

Our results suggest that, beyond spatial differences in the availability of food resources (Gambi et al., 2014), the life cycles and strategies of different components of the biota could play a key role in influencing their bathymetric patterns. Likewise, the different functional diversity and feeding targets of macrofauna and megafauna can be responsible for the differences in abundance and biomass observed in some selected deep-sea regions (van der Grient & Rogers, 2015; Witte et al., 2003). These differences can also hold true locally for specific

taxa belonging to the same group. For instance, previous studies conducted over the continental margins of the Mediterranean Sea reveal that some deep-sea species can be particularly abundant at specific bathymetric intervals (e.g., *Bathypterois mediterraneus* and deep-sea red shrimp *Aristeus antennatus*; D'Onghia, Lloris, Sion, Capezzuto, & Labropoulou, 2004; D'Onghia et al., 2009; Sardà et al., 2009). These species, thus, can influence the observed patterns of megafaunal abundance and biomass along bathymetric gradients (Baldrighi, Lavaleye, Aliani, Conversi, & Manini, 2014; Company et al., 2004; Sardà et al., 2009).

4.2 | Patterns of benthic biomass in the deep Mediterranean Sea

The decrease of meiofaunal biomass with increasing water depth is more pronounced in the Eastern than in the Western Basin. The different trophic conditions of the two basins, with food supply at 1,000 m depth up to 80 times higher in the Western than in the Eastern Basin (Danovaro et al., 1999), can explain the different patterns observed in the two basins. Our results suggest that the decrease of food supply with increasing water depth in regions with very low primary production (such as in the Eastern Basin) has a stronger effect on the benthic biomass than in regions displaying a higher primary production (such as the Western Basin). Meiofaunal individual size, indeed, significantly
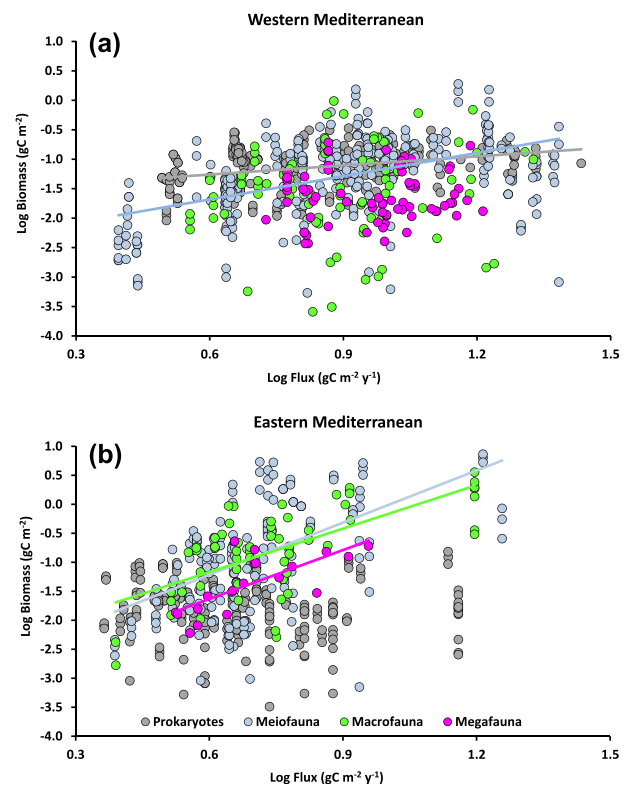

FIGURE 6 Relationship between biomass ($\log_{10}$-transformed, in grams of carbon per square metre) and organic carbon fluxes ($\log_{10}$-transformed, in grams of carbon per square metre per year) in the (a) Western and (b) Eastern Basins of the Mediterranean Sea. Only lines of significant relationships are reported (see Table 2)
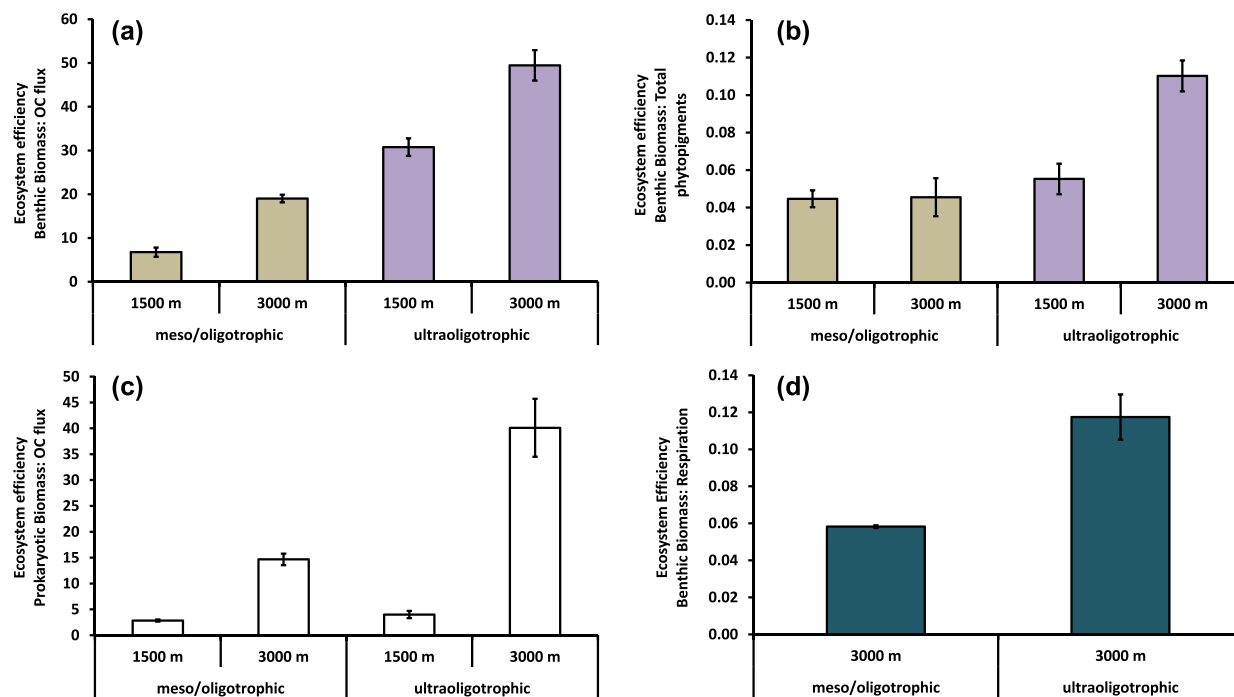
FIGURE 7 Ecosystem efficiency in different trophic conditions of the deep Mediterranean Sea. Reported is the ratio between (a) total benthic biomass and organic carbon (OC) flux (day), (b) total benthic biomass and total phytopigments (converted into C equivalents), (c) prokaryotic biomass and OC fluxes (day) and (d) total benthic biomass and benthic respiration (day)

decreases along the bathymetric gradient in both basins, with a rate that is higher in the Eastern than in the Western Basin (Supporting Information Appendix S3).

Given that body size is one of the most important properties of an organism and can be used to predict potential changes in deep-sea community structure (van der Grient & Rogers, 2015), our results suggest a shift of meiofaunal assemblages in the deepest sediments of the Mediterranean Sea towards more pronounced small-size r-strategy individuals. The r-strategists are characterized by short life cycles, fast colonization of defaunated systems, a small individual biomass and an opportunistic behaviour, whereas K-strategists are characterized by delayed maturity, low rates of reproduction, long life cycles and large individual biomass and are highly competitive in stable environmental conditions (Bongers, Alkemade, & Yeates, 1991). The mesotrophic/ultra-oligotrophic conditions of the deep Mediterranean Sea could favour the r-strategy species, because the organisms with smaller body size can cope better with food limitation than large organisms (DeLong, Okie, Moses, Sibly, & Brown, 2010).

In the Western Mediterranean, prokaryotic biomass shows a decreasing bathymetric pattern, whereas in the Eastern Mediterranean it increases with depth. The different substrate availability for prokaryotes in the two deep-sea basins can explain, in part, the observed different patterns. Sediments of the Western Basin show higher contents of bioavailable OC (*sensu* Danovaro, 2010) than those in the Eastern Basin (Gambi & Danovaro, 2006; Pusceddu, Dell'Anno, et al., 2009). The difference in food availability can promote differences in terms of repartitioning of biomass among different benthic components. For instance, the very low food supply in the Eastern Basin can support

prokaryotic growth, but is insufficient to sustain the development of the larger fauna as observed in the Western Basin. Moreover, viral abundance decreases with water depth in both basins, and more sharply in the Eastern Mediterranean, reflecting the patterns reported for their potential hosts.

Our findings also highlight that macrofauna represent the dominant component in the upper slope benthos, whereas prokaryotes dominate the total biomass below 2,000 m depth. This pattern indicates that the shift from metazoan to microbial dominance in total biomass, reported in the abyssal plains at the global scale (Rex et al., 2006; Wei et al., 2010), occurs at much shallower depths (i.e., bathyal plains) in the Mediterranean Sea. Accordingly, although the contribution of viruses to the total benthic biomass is always very low, it increases notably with depth. This result is consistent with the finding of increasing viral impact on deep-sea organisms (Corinaldesi, Dell'Anno, Magagnini, & Danovaro, 2010; Danovaro, Dell'Anno, et al., 2008; Dell'Anno et al., 2015), except, as reported above, for prokaryotes in the ultra-oligotrophic Eastern Basin.

Overall, our results reveal that the differences in food availability, size, life and feeding strategies characterizing the different benthic components can determine different responses to food depletion in terms of biomass of the various benthic groups.

4.3 | The deep Mediterranean Sea versus other oceanic regions

We report here that the rate of decline of meiofaunal abundance and biomass with water depth in the deep Mediterranean Sea is 2–4 times

higher than that reported for the global oceans (Rex et al., 2006; slopes for abundance: −0.0003 vs. −0.00007; slope for biomass: −0.0004 vs. −0.0002, in the Mediterranean Sea and in global oceans, respectively). We observed the same results for biomass estimated as milligrams of carbon per square metre according to Wei et al. (2010). The rate of decline of macrofaunal and megafaunal biomass with increasing water depth in the deep Mediterranean Sea is about half than that in the global oceans (−0.0002 vs. −0.0005, respectively, for macrofauna, and −0.0002 vs. −0.0004, respectively, for megafauna).

Our findings contrast with previous results, in which the decline of meiofauna with increasing water depth was generally sharper than the decline of macrofauna and megafauna (Rex et al., 2006; Wei et al., 2010). In the deep Mediterranean Sea, indeed, the rate of biomass decline with increasing water depth follows the order: meiofauna > macrofauna ≈ megafauna, whereas in the global oceans the order is macrofauna > megafauna > meiofauna. These differences could be explained by the peculiarly oligotrophic conditions of the deep Mediterranean Sea and the higher efficiency of larger benthic components in exploiting limited and interspersed food resources. In this regard, it is worth noting that the OC fluxes are generally much lower in the Mediterranean Sea than in other oceanic regions (Jones et al., 2014). This holds particularly for the Eastern Mediterranean Basin, which is one of the most oligotrophic regions worldwide (Psarra, Tselepides, & Ignatiades, 2000). In such food-limited conditions, our results reveal that meiofauna, macrofauna and megafauna are positively correlated with the OC fluxes, but meiofauna appear more vulnerable than macrofauna and megafauna to the reduction of OC inputs expected with the increasing of depth (Figure 6). Larger organisms require more energy in total, but less energy per unit of biomass (van der Grient & Rogers, 2015). This aspect along with the low metabolic rate of deep-sea organisms can be advantageous for larger organisms with specific feeding preferences (van der Grient & Rogers, 2015). Given the different energy requirement, it is possible that macrofauna and megafauna are able to respond better to the severe food limitation than meiofauna in the deep Mediterranean Sea. Moreover, larger benthic components display biological traits (e.g., life stages, reproduction, behaviour; Costello et al., 2015) and trophic strategies that allow them to move rapidly to search for food (Collins, Bailey, Ruxton, & Priede, 2005). In this regard, Witte et al. (2003) conducted *in situ* experiments in the North Atlantic Ocean showing that larger organisms can exploit the available resources more rapidly, taking metabolic advantage over smaller organisms.

Different factors (e.g., temperature and food availability) can explain the spatial patterns of benthic assemblages (including biodiversity) along bathymetric gradients in deep-sea ecosystems (McClain et al., 2012; Woolley et al., 2016). Our investigation reveals that food availability appears to be the main factor in driving the spatial patterns of benthic biomass in the deep Mediterranean Sea, as also demonstrated by the species–energy approach at the global oceanic scale (Woolley et al., 2016). Temperature appears to influence only the spatial patterns of the smaller benthic components (prokaryotes and meiofauna). This confirms for the deep Mediterranean Sea, where the

bottom water temperature is high and relatively constant across the basin (Emig & Geistdoerfer, 2004), the patterns observed at the global ocean scale, where temperature changes are much more relevant (from > 0 up to 15 °C; McClain et al., 2012).

Our results reveal that the peculiar trophic conditions of the deep Mediterranean Sea associated with a higher efficiency of larger benthic components in exploiting limited food resources can explain the greater decrease in meiofaunal biomass with increasing water depth compared with what is reported at the global scale.

4.4. | Efficiency of resource exploitation in the deep Mediterranean Sea

Among benthic groups, foraminifera can be an important component of the deep-sea food webs and for C cycling (Jeffreys, Burke, Jamieson, Narayanaswamy, & Ruhl, 2013; Nomaki, Heinz, Nakatsuka, Shimanaga, & Kitazato, 2005; Witte et al., 2003). *In situ* experiments based on an enrichment of food inputs reveal that foraminifera (at the size of both meiofauna and macrofauna) may rapidly ingest large amounts of carbon and, thus, can play an important role in carbon consumption in deep-sea ecosystems (Nomaki et al., 2005). However, the total biomass of foraminifera is negligible compared with that of prokaryotes. We acknowledge that the foraminifera could play a relevant role in benthic deep-sea ecosystems, but data of foraminiferal abundances from the deep Mediterranean Sea are very limited (Sabbatini et al., 2014). This is even more evident for their biomass, because of problems in determining the living fraction of this component (Borrelli et al., 2011). Data available from the Catalan margin suggest that the abundance of foraminifera (size > 150 μm) ranges between 7.6 and 17.0 individuals 10 cm^{-2} at 1,987 and 343 m depth, respectively (Fontanier et al., 2008). In the southern Adriatic Sea, the abundance of foraminifera varied from 18 to 251 individuals cm^{-2} at 1,131 and 210 m depth, respectively (Jorissen, de Stigter, & Widmark, 1995), suggesting that foraminiferal abundance is significantly lower than the metazoan meiofaunal abundance from the same areas at equal depths (Bianchelli, Gambi, Zeppilli, & Danovaro, 2010). Given the paucity of biomass data in the deep Mediterranean Sea, we omitted from our analysis the contribution of the foraminifera to benthic biomass.

The analysis of the ecosystem efficiency based on the ratio between benthic biomass and available resources reveals that the efficiency of exploitation of the fresh OC inputs increases significantly with increasing water depth. This pattern is consistent across different trophic conditions (mesotrophic/oligotrophic Western Basin versus ultra-oligotrophic Eastern Basin) in the deep Mediterranean Sea (Figure 7). Our results suggest that the deep-sea biota increases their efficiency in exploiting food sources up to 300% in extremely food-limited conditions. This means that deep-sea benthos in the Mediterranean Sea is able to provide a responsive adaptation to the decreasing of food with increasing depth, particularly in the deep Eastern Basin. The high efficiency of the deep-sea benthos in exploiting food sources is further confirmed by the higher ratio of benthic biomass to respiration in the ultra-oligotrophic sediments of the Eastern Mediterranean Sea. Among the different benthic components investigated, prokaryotes

largely contribute to the ecosystem efficiency, driving its increasing values along the bathymetric gradient. Our results suggest that the shift of biomass from larger to smaller components with the increasing of water depth is associated with a higher ecosystem efficiency.

Deep-sea ecosystems are extremely vulnerable to direct and indirect anthropogenic pressures, including temperature changes, food depletion, trawling and overfishing (Coll, Librato, Tudela, Palomera, & Pranovi, 2008; Pusceddu et al., 2014; Yasuhara & Danovaro, 2016), and increasingly, the need for ecological restoration and conservation of deep-sea ecosystems is being recognized (Barbier et al., 2014; van Dover et al., 2014). Available results and predictive models, indeed, suggest that global change and increasing sea-surface temperatures could significantly reduce the export of primary production to the deep sea (Jones et al., 2014). A reduction in primary production can influence the biomass, biodiversity and the metabolic rates of benthic communities (Jones et al., 2014; Smith et al., 2009; Woolley et al., 2016), including the microbial components (i.e., prokaryotes and viruses; Danovaro, Corinaldesi, & Dell'Anno, 2011; Kirchman, Anxelu, Morán, & Ducklow, 2009). The effects of food limitation on benthic ecosystems due to global change are expected for the Mediterranean Sea (Coma et al., 2009) even though episodic events related to climate anomalies (such as transients and dense shelf water cascading) can cause a fast accumulation of organic matter in deep-sea sediments and consequent shifts in the benthic biomass and biodiversity (Danovaro, Dell'Anno, & Pusceddu, 2004; Pusceddu et al., 2013).

Results presented here suggest that in the Mediterranean Sea benthic components, with a major role of smaller ones, during severe food limitation (which increases with increasing water depth), could partly cope with these conditions by increasing their efficiency in exploiting available resources. These findings raise the possibility that the peculiar response of the Mediterranean Basin is attributable to its characteristics as a 'miniature ocean' or could represent an anticipation of the effects of future global change in other systems. However, if the 'Mediterranean' response reported here occurs in other oceanic regions, the consequences of food limitation could possibly be less severe than expected in the deep-sea domain.

DATA ACCESSIBILITY

Data will be available as tables in the data repository of the MERCES project through Zenodo.

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BIOSKETCH

The Marine Biology and Ecology research team of the Department of Life and Environmental Sciences of the Polytechnic University of Marche is composed of an interdisciplinary group of scientists devoted to the investigation of different aspects of deep-sea biology and ecology, with a special focus on the understanding of the links between biodiversity and ecosystem functioning and of the management and protection of deep-sea habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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