1 # Functional response of deep-sea benthos to food limitation can
2 # reduce the impact of climate change on the deep sea

3

4 Running head : Deep-sea response to expected food limitation

5

6 Cristina Gambi[1]*, Cinzia Corinaldesi[1], Antonio Dell'Anno[1], Antonio Pusceddu[2], Gianfranco
7 D'Onghia[3], Anabella Covazzi-Harriague[4], Roberto Danovaro[1,5]

8

9 *[1] Università Politecnica delle Marche, Dipartimento di Scienze della Vita e dell'Ambiente,*
10 *60131 Ancona, Italy*

11 *[2] Dipartimento di Scienze della Vita e dell'Ambiente, 09126 Cagliari, Italy*

12 *[3]Università degli Studi di Bari Aldo Moro, Dipartimento di Biologia, 70125 Bari, Italy*

13 *[4]Università di Genova, Dipartimento per lo Studio del Territorio e delle sue Risorse, 16132*
14 *Genova, Italy*

15 *[5]Stazione Zoologica Anton Dohrn, 80121 Napoli, Italy*

16

17

19

20

21 ***Corresponding Author:**
22 Cristina Gambi
23 Dipartimento di Scienze della Vita e dell'Ambiente
24 Università Politecnica delle Marche
25 Via Brecce Bianche
26 60131 Ancona, Italy
27 Tel +39 071 2204331
28 Fax +39 071 2204650
29 c.gambi@univpm.it

30

33

34

Abstract:

Aim: A paradigm of deep-sea ecology is that the ocean interior is a food-limited environment which results in decreasing abundance and body size of fauna with increasing water depth. Here we estimated the efficiency of benthic biota in exploiting resources with increasing water depth to assess the potential response of deep-sea organisms to predictable changes in food availability as determined by global change.

Location: Mediterranean Sea.

Methods: We used the largest synoptic data set produced so far on abundance and standing stocks of benthic viruses, prokaryotes, meio-, macro- and megafauna from the Western to Eastern basins of the deep Mediterranean Sea, across depth and longitudinal gradients of food availability.

Results: Our analysis reveals that only meiofauna (both abundance and biomass) show a significant negative log-linear relationship with increasing water depth consistently in both basins and the whole Mediterranean Sea. Conversely, all other benthic components, from viruses to mega-fauna, show different/opposite bathymetric patterns. Our results also show that, beneath 2000m, the benthic biomass is dominated by prokaryotes and, conversely to patterns reported at global scale, meiofaunal biomass decreases with increasing water depth to a greater extent than do macro- and megafauna. The comparisons conducted among different trophic conditions (from meso/oligo- to ultra-oligotrophic, Western and Eastern basin, respectively) indicate that the efficiency of benthic ecosystems in exploiting organic carbon inputs increases with increasing depth, consistently in all investigated basins. In particular, the efficiency of exploitation of the "fresh" food resources is mainly driven by prokaryotes and increases (up to 300%) in the ultra-oligotrophic systems.

Main conclusions: Since global warming is expected to increase water column stratification, which, in turn, will alter organic carbon inputs to the deep seafloor, our results suggest that the effects of climate change on deep-sea assemblages could be partly counteracted by their higher efficiency in exploiting available resources.

Introduction

Benthic deep-sea ecosystems (beneath 200 m depth) cover 65% of the Earth surface (Danovaro *et al.*, 2014). The comprehension of their functioning and dynamics is a central issue in marine ecology and is essential to understand the processes of global carbon and nutrient cycling, and the response of these ecosystems to global change (Rowe & Pariente, 1992; Danovaro *et al.*, 2001; Danovaro *et al.*, 2014; Rogers, 2015).

Quantitative synoptic information on benthic prokaryotes, meiofauna, macrofauna and megafauna in the deep sea, under an "End-to-End" perspective, is limited to few meta-analyses which are based on data from studies conducted on specific benthic components (Rex *et al.*, 2006; Wei *et al.*, 2010 and literature therein). The consistent finding of these global scale meta-analyses is the decline of benthic abundance and biomass with increasing water depth, particularly evident for meio-, macro- and mega-fauna (Rex *et al.*, 2006; Wei *et al.*, 2010; Gambi et al., 2010; van der Grient & Rogers, 2015; Rogers, 2015). Such patterns are generally explained with the exponential decrease in organic matter supply with increasing water depth (Gage & Tyler, 1991; Smith *et al.*, 2008; Jones *et al.*, 2014). Analyses of abundance and biomass are also conducted on smaller benthic components (e.g., bacteria and protozoa; Boetius *et al.*, 1996; Soltwedel *et al.*, 2000; Danovaro *et al.*, 2002; Deming & Camperter, 2008), but, in those cases, the results reveal barely decreasing or invariant bathymetric patterns (Rex *et al.*, 2006; Wei *et al.*, 2010; Gooday & Jorissen, 2012).

Recent investigations carried out in the Pacific and Atlantic Oceans revealed the existence of close relationships between climate change, food limitation and decreasing deep-sea standing stocks (Ruhl *et al.*, 2008; Smith *et al.*, 2008; Yasuhara *et al.*, 2008; Smith *et al.*, 2009; Billet *et al.*, 2010; McClain *et al.*, 2012; Jones *et al.*, 2015).

88   The Mediterranean Sea represents less than ca. 1% of the ocean surface, but it is a hot spot

89   of biodiversity containing more than 7.5% of global marine biodiversity (Danovaro *et al.*,

90   2010). This sea is particularly exposed to the impact of climate change (Giorgi, 2006; Jordà *et*

91   *al.*, 2012), and is one of the marine regions worldwide with the highest increase of water

92   temperature in the last 50 years (Burrows *et al.*, 2011; Durrieu de Madron *et al.*, 2011).

93   Recent studies predict that global change, enhancing water column stratification through

94   increased sea surface temperature, might reduce the input of food resources to the deep

95   Mediterranean Sea benthos (Canals *et al.*, 2006; Coma *et al.*, 2009), though with some

96   differences among different deep-sea habitats (e.g., active canyons vs. open slopes; Pusceddu

97   *et al.*, 2013; Cartes *et al.*, 2015; Pusceddu *et al.*, 2016).

98   Here, we use the Mediterranean Sea as a model for evaluating the possible effects of

99   changes in food supply/availability, due to present and future climate change, on abundance

100   and standing stock of deep-sea benthic organisms. To do this, we collected the largest

101   synoptic data set produced so far for abundance and standing stock of viruses, prokaryotes,

102   meio-, macro- and mega-fauna along bathymetric and longitudinal trophic gradients of the

103   deep Mediterranean Sea. We also estimated the efficiency of benthic biota in exploiting

104   resources with increasing water depth to assess the potential response of deep-sea organisms

105   to predictable changes in food availability as determined by global change.

106

107 **Material and Methods**

108 *Study area: the Mediterranean Sea*

109 The deep Mediterranean Sea is divided into Western and Eastern basins by the Sicily channel.

110 The two regions, due to different freshwater inputs and nutrient supply, show major

111 differences in primary production, and thus in the export of organic matter to the deep-sea

112   floor (Danovaro *et al.*, 1999). The average depth of the Mediterranean Sea is about 1450m,

113   much shallower than the average depth of the world oceans (ca. 4 km).

114   The main features of the deep Mediterranean Sea are: (a) stable homeothermy from

115   roughly 300-500m down to the bottom, bottom temperatures of about 12.8°C to 13.5°C in the

116   Western basin, and 13.5°C to 15.5°C in the Eastern basin (Emig & Geistdoerfer, 2004), (b)

117   high oxygen concentrations of deeper water masses, (c) high variability in benthic trophic

118   state (from meso/oligo- to ultra-oligo-trophic conditions with an eastward decreasing

119   gradient, Gambi & Danovaro, 2006; Pusceddu *et al.*, 2009; Pusceddu *et al.*, 2010; Gambi *et*

120   *al.*, 2014), and organic matter inputs to the seafloor (15-80 times higher in the Western than in

121   the Eastern basin, Danovaro *et al.*, 1999), (d) a general decrease of biodiversity with depth,

122   especially for macro- and megafauna (e.g. Danovaro *et al.*, 2010).

123

124   *Benthic abundance and biomass*

125   We compiled a cumulative inventory of 1509 records of abundance and biomass of viruses,

126   prokaryotes, meiofauna, macrofauna and megafauna (including invertebrates and fishes)

127   obtained from new data and published results within the bathymetric interval 117-4394m in

128   the deep Mediterranean Sea (Supplemental Table S1; Figure 1).

129   Data of viruses, prokaryotes and meiofauna were produced by the same inter-calibrated

130   operators, using similar sampling devices and the same standardized protocols. Macro- and

131   megafauna data, instead, were obtained by different operators but using the same

132   methodologies, mesh size and approaches, thus minimizing the possible methodological bias.

133   The benthic foraminifera were not included in this investigation due to the limited

134   information of this component in the deep Mediterranean Sea and difficulties to estimate their

135   biomass (Soltwedel, 2000; Rex *et al.*, 2006; Wei *et al.*, 2010).

136

Carbon content associated to viral particles and prokaryotic biomass

138 Benthic viral abundances (expressed as viruses g^{-1} dry sediment) were determined on 265

139 samples collected in different sectors of the deep Mediterranean basin at depths ranging from

140 183 to 4347m. Viral abundances were converted into C content assuming a conversion factor

141 of 0.06 to 0.08 fg C $virus^{-1}$ (estimated for different benthic deep-sea ecosystems including the

142 Mediterranean Sea, Dell'Anno *et al.*, 2015). Such conversion factors are conservative since

143 they are much lower than those previously assumed for estimating the C content contained

144 into marine viruses (i.e. 0.2 fg C $virus^{-1}$; Wilhelm & Suttle, 1999; Suttle, 2007).

145 Benthic prokaryotic abundances (expressed as number of cells g^{-1} dry sediment) were

146 determined on 508 samples collected in different sectors of the deep Mediterranean basin at

147 depths ranging from 183 to 4347m. Prokaryotic biomass was estimated from prokaryotic

148 biovolume converted to C content assuming 310 fg C μm^3 (Danovaro *et al.*, 2008a). Viral and

149 prokaryotic abundance and biomass were then normalized to unit of sediment surface (i.e.,

150 m^2) assuming a sediment density of 1.8 and an average sediment water content of 50%

151 (Dell'Anno & Danovaro, 2005).

152

Meiofauna

154 The meiofaunal data set included 501 records for abundance and biomass, respectively from

155 the Western to the Eastern Mediterranean basins at depths ranging from 183 to 4345m.

156 Meiofaunal abundance was reported as individuals m^{-2}. Meiofaunal biomass was obtained

157 from individual biomass of specimens belonging to the different taxa (Danovaro, 2010). For

158 nematodes, body mass was calculated from the biovolume which was estimated using the

159 Andrassy (1956) formula ($V=L \times W^2 \times 0.063 \times 10^{-5}$, in which body length is L, and the width is

160   W). The biovolume of all other taxa were derived from measurements of body length (L, in

161   mm) and width (W, in mm), using the formula $V = L \times W^2 \times C$, where C is the approximate

162   conversion factor for each metazoan meiofaunal taxon (Feller & Warwick, 1988). Each body

163   volume was multiplied by an average density (1.13 g cm^{-3}) to obtain the biomass (µg dry

164   weight) assuming that the dry:wet weight ratio is 25%, and that C content accounts for 40%

165   of the dry weight (Feller & Warwick 1988). Data of C biomass measured according to Jensen

166   (1984) have been recalculated according to Feller & Warwick (1988). Meiofaunal biomass

167   was reported as gC m^{-2}.

168

169   *Macrofauna and megafauna*

170   The data sets of macro- and mega-faunal abundance and biomass (expressed as individuals m^{-2}

171   and gC m^{-2}, respectively) included 143 and 92 records, respectively, and covered different

172   sectors of the deep Mediterranean Sea at depths ranging from 117 to 4394m. Macro and

173   megafaunal organisms were weighed to obtain the biomass value expressed as DW (oven-

174   drying at 60°C for 24 h). The biomass of each group was standardized to the C content using

175   appropriate conversion factors reported in the literature (Rowe, 1983; Feller & Warwick,

176   1988; Ricciardi & Bourget, 1998; Soltwedel, 2000; Galeron *et al.*, 2000).

177

178   *Benthic standing stock in the whole Mediterranean basin*

179   Values of biomass were also estimated for the whole extension of the Mediterranean seafloor

180   at the depth interval 200-4000m as the sum of the total biomass estimated for the extension of

181   the seafloor at selected depth intervals: 200-1000m, 1000-2000m, 2000-3000m, 3000-4000m

182   (Danovaro *et al.*, 2010). Values below 4000m were excluded since the extension of the

183 seafloor below 4000m represents less than 1% of the entire Mediterranean basin (Danovaro *et*

184 *al.*, 2010).

185

186 *Organic carbon inputs and total phytopigments in deep-sea sediments*

187 As a proxy of the inputs of organic matter to the deep-sea benthos we used data of organic

188 carbon (OC) fluxes from a selection of sites across depth and longitudinal gradients of food

189 availability in the deep Mediterranean Sea. The selected deep-sea sites were at 1500m and

190 2000m in the Catalan margin (Northern-Western Mediterranean, Sanchez-Vidal *et al.*, 2009),

191 at 1500m in the Northern Cretan margin (Eastern Mediterranean, Stavrakakis *et al.*, 2000) and

192 at ca 3000m in the bathyal plains of the Western and Eastern basins (Gambi & Danovaro,

193 2006; Zuniga *et al.*, 2008). Data of OC fluxes were collected by sediment traps deployed ca

194 30m above the seafloor and average values on daily basis (mgC m^{-2} d^{-1}) were calculated from

195 OC fluxes collected over a period of one year.

196   As a proxy of freshly deposited material in deep-sea sediments we used sedimentary

197 contents of total phytopigments, once converted into C equivalents as outlined in Danovaro

198 (2010).

199

200

201 *Ecosystem Efficiency*

202 Two independent indicators of ecosystem efficiency were utilized: the ratio of benthic

203 biomass to OC fluxes and the ratio of benthic biomass to freshly deposited organic C

204 estimated from total phytopigment sedimentary contents once converted into C equivalents

205 (Danovaro *et al.*, 2008b). Benthic biomass (as the sum of the contribution of prokaryotes,

206 meio-, macro and megafauna) was compared to values of organic C fluxes and freshly

8

207 deposited organic C to the deep-sea floor at selected areas located at 1500m, 2000m and

208 3000m in the Western basin and 1500m and 3000m depth in the Eastern basin. These areas

209 were selected as they are characterized by important changes in trophic conditions spanning

210 from meso/oligotrophic to ultra-oligotrophic in the Western and Eastern Mediterranean basin,

211 respectively.

212

213 *Data analysis*

214 To examine the relationships between abundance and standing stocks *vs.* depth, maintaining

215 constant latitude and longitude, we used a partial regression analysis according to the

216 approach reported in Rex *et al.* (2006) and Wei *et al.* (2010). The multiple regression

217 residuals of abundance and standing stocks against latitude and longitude were used as

218 dependent variables to regress against water depth. To bring the dependent variable back to an

219 appropriate scale, the y-intercept from the multiple regression was added to the residuals.

220

221 **Results**

222 *Bathymetric patterns of abundance and biomass*

223 Our analysis shows that, among all of the investigated benthic components, only meiofauna

224 show a significant negative log-linear relationship between the abundance and the water depth

225 consistently in the whole Mediterranean Sea and in the Western and Eastern basins (Figure

226 2a; Table 1). All other investigated benthic components show different and regionally

227 variable bathymetric patterns. In the Western Mediterranean, the abundance of prokaryotes

228 and megafauna significantly decreases with increasing water depth, while macrofauna

229 significantly increase and viruses do not change (Figure 2b; Table 1). In the Eastern basin, all

230 components, except for megafauna, display significant log-linear relationships between

231   abundance and water depth, but these are negative for viruses and macrofauna, and positive

232   for prokaryotes (Figure 2c; Table 1).

233   Significant and negative log-linear relationships between the biomass of all components,

234   except for viruses and prokaryotes, and the water depth are observed in the whole

235   Mediterranean Sea (Figure 3a; Table 1). In the Western basin only the biomass of prokaryotes

236   and meiofauna significantly decreases with increasing water depth (Figure 3b; Table 1). In the

237   Eastern basin, viral, meio- and macrofaunal biomass displays significant negative

238   relationships with water depth, whereas prokaryotic biomass increases along the bathymetric

239   gradient (Figure 3c; Table 1).

240   The meiofaunal individual biomass reveals consistent significant and negative log-linear

241   relationships with the increasing water depth in both Mediterranean basins (Figure 4a,b).

242   The analysis of the contribution of each benthic component to the total benthic biomass

243   reveals that different groups dominate the total benthic biomass at different bathymetric

244   ranges (Figure 5). Macrofauna dominate above 1000m depth (representing ca 41% of the total

245   benthic biomass), macrofauna and meiofauna (ca 31 and 35%, respectively) co-dominate

246   between 1000 and 2000m depth, whereas prokaryotes (73-88%) become largely dominant

247   below 2000m depth. The contribution of viruses to the total benthic biomass is almost

248   negligible at the shallower depth ranges, but ca 1% below 3000m depth.

249   Overall, the total benthic biomass in the deep Mediterranean basin (depth range 200-

250   4000m) is estimated in ca. 0.34 Mt C and is largely accounted by the stock resident in the

251   depth interval from 200 to 1000m (ca. 52%), followed by the one in the depth interval from

252   1000 to 2000 m (ca. 30%) (Supplemental Table S2).

253

254

255   *Relationship between faunal biomass and OC fluxes and ecosystem efficiency*

256   Both meio- and macro-fauna show significant positive relationships between OC inputs and

257   biomass in both Mediterranean basins. The rate of increasing biomass with the increasing of

258   OC fluxes is generally steeper for meiofauna than macrofauna and the rates are generally

259   higher in the ultra-oligotrophic than meso/oligotrophic systems (Figure 6a,b).

260   Ecosystem efficiency, estimated as the ratio of total benthic biomass to OC fluxes, increases

261   with the increasing of water depth in both the meso/oligotrophic (Western) and ultra-

262   oligotrophic (Eastern) Mediterranean basins (Figure 7a). The same pattern is confirmed in the

263   Eastern basin using the ecosystem efficiency estimated as the ratio of benthic biomass to

264   freshly deposited organic C as total phytopigments, while the ecosystem efficiency remains

265   invariant in the Western basin (Figure 7b). Overall, among the different benthic components

266   investigated, the ecosystem efficiency is mainly driven by the contribution of prokaryotes

267   (Figure 7c). This pattern is also confirmed when the efficiency is estimated as the ratio

268   between prokaryotic biomass and total phytopigments converted into C equivalents (data not

269   shown).

270

271   **Discussion**

272   *Abundance and standing stock in the deep Mediterranean Sea*

273   The decline of abundance and standing stocks with increasing water depth is typically

274   explained with the decreased availability of food sources (Rowe, 1983; Gage & Tyler 1991;

275   Rex *et al.*, 2006; Wei *et al.*, 2010). Previous studies highlighted that such a response is more

276   pronounced for megafaunal components than for macro- and meio-fauna, to become

277   negligible for microbial components (Rex *et al.*, 2006).

278   Results reported here allow comparing the bathymetric patterns of different benthic

279   components, from viruses to megafauna, using the largest synoptic dataset of abundance and

280   biomass collected so far in the Mediterranean Sea, with data available at global scale. We

281   report here that the abundance and biomass of the various benthic components respond

282   differently to the decreasing food availability in the Mediterranean Sea, but also report

283   notable differences with the patterns already observed at global scale (Rex *et al.*, 2006; Wei *et*

284   *al.*, 2010). Our findings disconfirm the general statement by which all benthic components

285   decline with increasing water depth at global scale (Rex *et al.*, 2006; Wei *et al.*, 2010), and

286   reveal that in the Mediterranean Sea abundance and biomass of the different benthic

287   components show variable patterns with water depth. Only meiofauna display a consistent

288   significant negative relationship with water depth (for both abundance and biomass), whereas

289   all other benthic components (including viruses and prokaryotes) remain unvaried, or

290   increase. These results suggest that, beyond spatial differences in the availability of food

291   resources, also the life cycles and life strategies of different components of the biota could

292   play a key role in influencing their bathymetric patterns. Similarly, the different functional

293   diversity and feeding targets of macrofauna and megafauna can be responsible for the

294   differences in abundance and biomass observed in some selected deep-sea regions (Rex &

295   Etter, 1998; Witte *et al.*, 2003, van der Grient & Rogers, 2015). These differences can locally

296   hold also for specific taxa belonging to the same group. For instance, previous studies

297   conducted over the continental margins of the Mediterranean Sea revealed that some deep-sea

298   species can be particularly abundant at specific bathymetric intervals (e.g., *Bathypterois*

299   *mediterraneus*, D'Onghia et al., 2004a; deep-sea red shrimp *Aristeus antennatus,* D'Onghia et

300   al., 2009; *Sardà et al.*, 2009), thus influencing the observed patterns of megafaunal abundance

301   and biomass (Company *et al.*, 2004; D'Onghia *et al.*, 2004b; Ramirez *et al.*, 2008; Sardà *et*

302   *al.*, 2009, Baldrighi *et al.*, 2014).

303   When the log-linear negative relationships are compared, the decrease of meiofaunal

304   biomass with increasing water depth is higher in the Eastern than in the Western basin. This is

305   most likely linked to the different trophic conditions of the two basins, with food supply at

306   1000m depth up to 80 times higher in the Western than in the Eastern basin (Danovaro *et al.*,

307   1999). These results suggest that the decrease of food supply with increasing water depth has

308   a stronger effect on the benthic biomass of highly oligotrophic regions (such as the Eastern

309   Mediterranean basin) than in meso/oligotrophic systems (such as the Western Mediterranean

310   basin).

311   Moreover, the decline of meiofaunal biomass with increasing water depth was more

312   evident than the decline of abundance, suggesting that the reduction of food supply to the

313   deep sea can contribute to determine a shift of benthic community structure, by increasing the

314   relevance of individuals with small body size. This is confirmed by the significant decreasing

315   of the meiofaunal individual size along the bathymetric gradient in both basins with a rate of

316   decreasing higher in the Eastern than Western basin (Figure 4). Since the body size is one of

317   the most important properties of an organism and can be used to predict potential changes in

318   deep-sea community structure (Ruhl *et al.*, 2008; Kuhnz *et al.*, 2014; Van der Grient &

319   Rogers, 2015) our results suggest a shift of meiofaunal assemblages towards a more

320   pronounced small-size r-strategy individuals in deep Mediterranean Sea.

321   In the Western Mediterranean, prokaryotes (in terms of biomass) showed a decreasing

322   bathymetric pattern, whereas in the Eastern Mediterranean increased with depth. This

323   difference can be partially explained in terms of the different substrate availability for

324   prokaryotes in the two deep-sea basins. In the sediments of the oligo/mesotrophic Western

325   basin organic matter shows higher contents and higher bioavailability than the one in the

326   Eastern ultra-oligotrophic basin (Gambi & Danovaro, 2006; Pusceddu *et al.*, 2010). This,

327   most likely, facilitates prokaryotes in the Eastern basin, but larger fauna in the Western one.

328   On the other hand, viruses decreased in both basins, and even more sharply in the Eastern

329   Mediterranean. Therefore, the different bathymetric patterns of prokaryotic biomass in the

330   two basins could be also explained by a reduced top-down control exerted by viruses in the

331   highly oligotrophic Eastern basin compared to the one in the meso/oligotrophic Western basin

332   (Danovaro *et al.* 2008a; Fonda Umani *et al.*, 2010). Our data also highlight the presence of

333   shifts in the relative contribution to the total biomass of the different benthic components:

334   macrofauna represent the dominant biotic component of the upper slope (200-1000m depth),

335   whereas below 2000m depth the total biomass is dominated by the prokaryotes. This indicates

336   that the shift from metazoan to microbial dominance, reported in the abyssal plains at global

337   scale (Rex *et al.*, 2006; Wei *et al.*, 2010), occurs at much shallower depths (i.e., bathyal

338   plains) in the Mediterranean Sea. Accordingly, although the contribution of viral biomass to

339   the total benthic biomass is always very low, it increases notably with depth. This result is

340   consistent with the finding of increasing viral impact on deep-sea organisms (Danovaro *et al.*,

341   2008a; Corinaldesi *et al.*, 2007; -2010; Dell'Anno *et al.*, 2015), except, as reported above, for

342   prokaryotes in the ultra-oligotrophic deep Eastern Mediterranean basin.

343

344   *The deep Mediterranean Sea vs. other oceanic regions*

345   We report here that the rate of decline of meiofaunal abundance and biomass with water depth

346   in the deep Mediterranean Sea is 2 to 4 times higher than that reported for the global oceans

347   (Rex *et al.*, 2006, slopes for abundance: -0.0003 vs -0.00007; slope for biomass: -0.0004 vs -

348   0.0002, in the Mediterranean Sea and in global oceans, respectively). The same results are

349   observed for biomass estimated as mg C m^{-2} according to Wei *et al.* (2010).

350   The rate of decline of macrofauna and megafauna biomass with increasing water depth in

351   the deep Mediterranean Sea is about half than that in the global oceans (-0.0002 vs. -0.0005,

352 respectively for macrofauna and -0.0002 vs -0.0004, respectively for megafauna). Our

353 findings contrast also with previous results in which the decline of meiofauna with increasing

354 water depth was generally sharper than the decline of macro- and megafauna (Rex *et al.*,

355 2006; Wei *et al.*, 2010). In the deep Mediterranean Sea, indeed, the rate of biomass decline

356 with increasing water depth is higher for meiofauna than for macro- and mega-fauna

357 (characterized by very similar slopes) with the following order: meiofauna > macrofauna ≈

358 megafauna, whereas in the global oceans the order is macrofauna > megafauna > meiofauna.

359 The reasons by which the meiofauna decrease to a greater extent than macro- and mega-

360 fauna in the Mediterranean Sea compared to other oceanic regions, could be the peculiarly

361 oligotrophic conditions of the deep Mediterranean Sea, and the higher efficiency of larger

362 benthic components in exploiting limited and interspersed food resources. In this regard it is

363 worth noting that the Mediterranean Sea is characterized by OC fluxes generally much lower

364 than values observed in other oceanic regions (Rex *et al.*, 2006; Rowe *et al.*, 2008; Wei *et al.*,

365 2010). This holds particularly for the Eastern Mediterranean basin, which is one of the most

366 oligotrophic regions worldwide (Psarra *et al.*, 2000; Pusceddu *et al.*, 2010). In such food-

367 limited conditions, our results reveal that both meio- and macrofauna are positively correlated

368 to the OC fluxes but meiofauna appear more vulnerable than macrofauna to the reduction of

369 OC inputs expected with the increasing of depth (Figure 6). Larger organisms require more

370 energy in total, but they require less energy per unit biomass and, combined with the low

371 metabolic rate in deep-sea organisms, it may prove advantageous to be larger for certain

372 feeding styles (Van der Grient & Rogers, 2015).This allows to hypothesize that macro- (and

373 mega)fauna are able to better cope with the severe food limitation than meiofauna in the deep

374 Mediterranean Sea. Moreover larger benthic components display biological traits and trophic

375 strategies that allow them to move rapidly to search for food (Collins *et al.*, 2005). Witte *et al.*

376 (2003) conducted *in situ* experiments in the North Atlantic Ocean showing that larger

15

377 organisms can exploit more rapidly the available resources, taking metabolic advantage over

378 smaller organisms.

379

380 *Resource exploitation efficiency in the deep Mediterranean Sea*

381 Our measurements of benthic biomass and available resources reveal that the efficiency in

382 exploiting fresh inputs of organic C increases significantly with increasing water depth. This

383 pattern is consistent across different trophic conditions (meso/oligotrophic Western basin *vs*.

384 ultra-oligotrophic Eastern basin) in the deep Mediterranean Sea (Figure 7). When these

385 patterns are compared with the OC fluxes from the water column, our results suggest that the

386 efficiency of the deep-sea biota in exploiting the available food sources increases significantly

387 (up to 300%) especially in extreme food limited conditions. This means that benthic

388 components are able to "positively" react to the decreasing of food inputs with the increasing

389 of depth in the Mediterranean Sea and their ability appears particularly evident in deep-sea

390 sediments in which the resources are typically scant (Eastern basin). Among the different

391 benthic components investigated, prokaryotes largely contribute to the ecosystem efficiency

392 driving its increasing values along the bathymetric gradient. Our results suggest that the shift

393 of biomass from larger to smaller components with the increasing of water depth is also

394 associated to an increasing of the ecosystem efficiency through the key role of prokaryotes in

395 the functioning of deep-sea ecosystems.

396   Deep-sea ecosystems are extremely vulnerable to a wide range of factors as direct and

397 indirect anthropogenic pressures including: temperature changes, food depletion, trawling and

398 overfishing (Yasuhara *et al.*, 2008; Coll *et al.*, 2008; Smith *et al.*, 2009; Swartz *et al.*, 2010;

399 Van Dover, 2011; Pham *et al.*, 2014; Pusceddu *et al.*, 2014; Yasuhara & Danovaro, 2014).

400 Available results and predictive models, indeed, suggest that global change and increasing

401 sea-surface temperatures could significantly reduce the export of primary production to the

402 deep sea (Smith *et al.*, 2008; Ruhl *et al.*, 2008; Jones *et al.*, 2014), thus influencing the

403 biomass and the metabolic rates of benthic communities (Yasuhara *et al.*, 2008; Smith *et al.*,

404 2009; Jones *et al.*, 2014), including also the smaller components (i.e., prokaryotes and

405 viruses; Kirchman *et al.*, 2009; Danovaro *et al.*, 2011). The effect of reduction of food supply

406 to benthic ecosystems is expected for the Mediterranean Sea (Coma *et al.*, 2009) even though

407 all expected effects of global change might be alternate to episodic events (such as transients

408 and dense shelf water cascading) that can cause a fast accumulation of organic matter in deep-

409 sea sediments and consequent shifts in deep-sea benthic biomass and biodiversity (Danovaro

410 *et al.*, 2001; -2004; Canals *et al.*, 2006; Pusceddu *et al.*, 2013).

411 Results presented here for the Mediterranean Sea suggest that benthic components with a

412 preeminent role of smaller ones, under severe food limitation (which increases with

413 increasing water depth), could partly cope with these conditions by increasing their efficiency

414 in exploiting available resources.

415 Our results open the question of whether the peculiar response of Mediterranean basin is

416 due to its characteristics of "miniature ocean" or could represent an anticipation of the effects

417 of future global change in other systems. However, if the "Mediterranean" response reported

418 here would reflect the one of other oceanic regions, the consequences of food limitation could

419 be possibly less severe than expected in the deep-sea domain.

420

425

426   **References**

427   Andrassy I (1956) The determination of volume and weight of nematodes. Acta Zoologica
428   (Hungarian Academy of Science), 2, 1-15.

429   Baldrighi E, Lavaleye M, Aliani S, Conversi A, Manini E (2014) Large spatial scale
430   variability in bathyal macrobenthos abundance, biomass, a- and b-diversity along the
431   Mediterranean continental margin. Plos One, 9(9), e107261.

432   Boetius A, Scheibej S, Tselepides A, Thiel H (1996). Microbial biomass and activities in
433   deep-sea sediments of the Eastern Mediterranean: trenches are benthic hotspots. Deep Sea
434   Research I, 43(9), 1439–1460.

435   Burrows MT, Schoeman DS, Buckley LB *et al.* (2011) The Pace of Shifting Climate in
436   Marine and Terrestrial Ecosystems. Science, 334 (6056), 652-655.

437   Collins MA, Bailey DM, Ruxton GD, Priede IG (2005) Trends in body size across an
438   environmental gradient: a differential response in scavenging and non-scavenging
439   demersal deep-sea fish. Proceedings of the Royal Society B: Biological Sciences, 272,
440   2051–2057.

441   Coma R, Ribes M, Serrano E, Jiménez E, Salat J, Pascual J (2009) Global warming-enhanced
442   stratification and mass mortality events in the Mediterranean. Proceedings of the National
443   Academy of Sciences of the United States of America, 106(15), 6176–6181.

444   Canals M, Puig P, Heussner S, Durrieu de Madron X, Palanques A, Fabres J (2006) Flushing
445   submarine canyons. Nature, 444 (7117), 354-357.

446   Cartes, J.E., Maynou, F., Fanelli, E., López-Pérez, C., Papiol, V., 2015. Changes in deep-sea
447   fish and crustacean communities at 1000–2200 m in the Western Mediterranean after
448   25years: Relation to hydro-climatic conditions. Journal of Marine Systems 143, 138–153.

449   Coll M, Librato S, Tudela S, Palomera I, Pranovi F (2008) Ecosystem overfishing in the

450   ocean. Plos One, 3(12), e3881.

451   Company JB, Maiorano P, Tselepides A, Politou C-Y, Plaity W, Rotllant G, Sardà F (2004)

452   deep-sea decapod crustaceans in the western and central Mediterranean Sea: preliminary

453   aspects of species distribution, biomass and population structure. Scientia marina, 68(3),

454   73-86

455   Corinaldesi C, Dell'Anno A, Danovaro R (2007) Viral infection plays a key role in

456   extracellular DNA dynamics in marine anoxic systems. Limnology and Oceanography 52,

457   508–516.

458   Corinaldesi C, Dell'Anno A, Magagnini M, Danovaro R (2010) Viral decay and viral

459   production rates in continental-shelf and deep-sea sediments of the Mediterranean Sea.

460   FEMS Microbiology Ecology, 72, 208-218.

461   Danovaro (2010) *Methods for the Study of Deep-Sea Sediments, Their Functioning and*

462   *Biodiversity*, CRC Press, Boca Raton.

463   Danovaro R, Corinaldesi C, Dell'Anno A, *et al.* (2011) Marine viruses and global climate

464   change. FEMS Microbiology Reviews, 35(6), 993–1034.

465   Danovaro R, Manini E, and Dell'Anno A (2002) Higher abundance of bacteria than of viruses

466   in deep Mediterranean sediments. Applied Environmental Microbiology 68, 1468–1472.

467   Danovaro R, Company JB, Corinaldesi C, *et al.* (2010) Deep-sea biodiversity in the

468   Mediterranean sea: the known, the unknown, and the unknowable. PloS One, 5(8), e11832.

469   Danovaro R, Dell'Anno A, Corinaldesi C, Magagnini M, Noble R, Tamburini C, Weinbauer

470   M (2008a) Major viral impact on the functioning of benthic deep-sea ecosystems. Nature,

471   454, 1084-1087.

472   Danovaro R, Dinet A, Duineveld G, Tselepides A (1999) Benthic response to particulate

473   fluxes in different trophic environments: a comparison between the Gulf of Lions-Catalan

474   Sea (western-Mediterranean) and the Cretan Sea (eastern-Mediterranean). Progress in

475   Oceanography, 44, 287–312.

476   Danovaro R, Gambi C, Dell'Anno A, Corinaldesi C, Fraschetti S, Vanreusel A, Vincx M,

477   Gooday AJ (2008b) Exponential decline of Deep-Sea Ecosystem Functioning Linked to

478   Benthic Biodiversity loss. Current Biology, 18, 1-8.

479   Danovaro R, Snelgrove P, Tyler P (2014) Challenging the paradigms of deep-sea ecology.

480   Trends in Ecology and Evolution, 29(8), 465–475

481   Danovaro R, Dell'Anno A, Fabiano M, Pusceddu A, Tselepides A (2001) Deep-sea

482   ecosystem response to climate changes: the eastern Mediterranean case study. Trends in

483   Ecology and Evolution, 16(9), 505-510.

484   Danovaro R, Dell'Anno A, Pusceddu A (2004) Biodiversity response to climate change in a

485   warm deep sea. Ecology Letters, 7, 821–828.

486   Dell'Anno A and Danovaro R (2005). Extracellular DNA plays a key role in deep-sea

487   ecosystem functioning. Science, 309(5744), 2179.

488   Dell'Anno A, Corinaldesi C, Danovaro R (2015) Virus decomposition provides an important

489   contribution to benthic deep-sea ecosystem functioning. Proceedings of the National

490   Academy of Sciences of the United States of America, 112(16), 2014–2019.

491   Deming JW, Carpenter SD (2008) Factors influencing benthic bacterial abundance, biomass,

492   and activity on the northern continental margin and deep basin of the Gulf of Mexico.

493   Deep Sea Research Part II, 55(24–26), 2597–2606.

494   D'Onghia G, Lloris D, Sion L, Capezzuto F, Labropoulou M (2004a) Observations on the

495   distribution, population structure and biology of *Bathypterois mediterraneus* Bauchot,

496   1962 in three areas of the Mediterranean Sea. Scientia Marina, 68 (Suppl. 3), 163-170.

497   D'Onghia G, Maiorano P, Capezzuto F, Carlucci R, Battista D, Giove A, Sion L, Tursi A,

498   (2009) Further evidences of deep-sea recruitment of *Aristeus antennatus* (Crustacea:

499   Decapoda) and its role in the population renewal on the exploited bottoms of the

500   Mediterranean. Fisheries Research 95 (2-3), 236-245.

501   D'Onghia G, Politou C-Y, Bozzano A, Lloris D, Rotlant G, Sion L, Mastrototaro F (2004b)

502   Deep-water fish assemblages in the Mediterranean Sea. Scientia Marina 68 (Suppl. 3), 87-

503   99.

504   Durrieu de Madron X, *et al.* (2011) Marine ecosystems' responses to climatic and

505   anthropogenic forcings in the Mediterranean. Progress in Oceanography, 91, 97–166.

506   Emig CC, Geistdoerfer P (2004) The Mediterranean deep-sea fauna: Historical evolution,

507   bathymetric variations and geographical changes, Carnets de Geologie/Notebooks on

508   Geology, Maintenon, Article 2004/01 (CG2004_A01_CCE-PG).

509   Feller RJ, Warwick RM (1988) Energetics. In *Introduction to the study of meiofauna* (Higgins

510   RP, Thiel H Eds) Smithsonian Institution Press, London, 181–196

511   Fonda Umani S, Malisana E, Focaracci F, Magagnini M, Corinaldesi C, Danovaro R (2010)

512   Disentangling the effect of viruses and nanoflagellates on prokaryotes in bathypelagic

513   waters of the Mediterranean Sea. Marine Ecology Progress Series, 418, 73–85.

514   Gage JD, Tyle PA (1991) *Deep-sea biology: a natural history of organism at the deep-sea*

515   *floor*. Cambridge University Press, 504p

516   Galeron J, Sibuet M, Mahaut M-L, Dinet A (2000) Variation in structure and biomass of the

517   benthic communities at three contrasting sites in the tropical Northeast Atlantic. Marine

518   Ecology Progress Series 197, 121-137.

519   Gambi C, Danovaro R (2006) A multiple-scale analysis of metazoan meiofaunal distribution

520   in the deep Mediterranean Sea. Deep Sea Research I, 53(7), 1117–1134.

521   Gambi C, Lampadariou N, Danovaro R (2010) Latitudinal, longitudinal and bathymetric

522   patterns of abundance, biomass of metazoan meiofauna: importance of the rare taxa and

523   anomalies in the deep Mediterranean Sea. Advances in Oceanography and Limnology,

524   1(1), 167-197.

525   Gambi C, Pusceddu A, Benedetti-Cecchi L, Danovaro R (2014) Species richness, species

526   turnover and functional diversity in nematodes of the deep Mediterranean Sea: searching

527   for drivers at different spatial scales. Global Ecology and Biogeography 23, 24–39.

528   Giorgi F (2006) Climate change hot-spots. Geophysical research letters, 33, L08707.

529   Gooday AJ, Jorissen FJ (2012) Benthic foraminiferal biogeography: controls on global

530   distribution patterns in deep-water settings. Annual Review of Marine Science, 4, 237-262.

531   Jensen P (1984) Measuring carbon content in nematodes. Helgolander Meeresunter-

532   suchungen, 38, 83-86.

533   Jones DOB, Yool A, We L-C, Henson SA, Ruhl HA, Watson RA, Gehlen M (2014) Global

534   reductions in seafloor biomass in response to climate change. Global Change Biology, 20,

535   1861–1872.

536   Jordà G, Marbà N, Duarte CM (2012) Mediterranean seagrass vulnerable to regional climate

537   warming. Nature climate change 2, 821–824.

538   Kirchman DL, Anxelu X, Morán G, Ducklow H (2009). Microbial growth in the polar oceans

539   role of temperature and potential impact of climate change. Nature Reviews, 7, 451−9.

540   Kuhnz LA, Ruhl HA, Huffard CL, Smith Jr KL (2014) Rapid changes and long-term cycles in

541   the benthic megafaunal community observed over 24 years in the abyssal northeast Pacific.

542   Progress in Oceanography 124, 1–11.

543   McClain CR, Allen AP, Tittensor DP, Rex MA (2012) Energetics of life on the deep seafloor.

544   Proceedings of the National Academy of Sciences of the United States of America, 109,

545   15366-15371.

546   Pham CK, Ramirez-Llodra E, Alt CHS, Amaro T, Bergmann M, Canals M, *et al.* (2014)

547   Marine Litter Distribution and Density in European Seas, from the Shelves to Deep Basins.

548   PLoS One, 9(4), e95839.

549   Psarra S, Tselepides A, Ignatiades L (2000) Primary productivity in the oligotrophic Cretan

550   Sea (NE Mediterranean): Seasonal and interannual variability. Progress in Oceanography,

551   46, 187–204.

552   Pusceddu A, Gambi C, Zeppilli D, Bianchelli S, Danovaro R (2009) Organic matter

553   composition, metazoan meiofauna and nematode biodiversity in Mediterranean deep-sea

554   sediments. Deep Sea Research II, 56 (11–12), 755–762.

555   Pusceddu A, Bianchelli S, Canals M, Sanchez-Vidal A, De Madron XD, Heussner S,

556   Lykousis V, de Stigter H, Trincardi F, Danovaro R (2010) Organic matter in sediments of

557   canyons and open slopes of the Portuguese, Catalan, Southern Adriatic and Cretan Sea

558   margins. Deep-Sea Research I, 57, 441–457.

559   Pusceddu A, Mea M, Canals M, Heussner S, Durrieu De Madron X, Sanchez-Vidal A,

560   Bianchelli S, Corinaldesi C, Dell'Anno A, Thomsen L, Danovaro R (2013) Major

561   consequences of an intense dense shelf water cascading event on deep-sea benthic trophic

562   conditions and meiofaunal biodiversity. Biogeosciences, 10, 2659-2670.

563   Pusceddu A, Bianchelli S, Martin J, Puig P, Palanques A, Masque P, Danovaro R (2014)

564   Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem

565   functioning. Proceedings of the National Academy of Sciences of the United States of

566   America, 111(24), 8861-8866.

567   Pusceddu A, Carugati L, Gambi C, Mienert J, Petania B, Sanchez-Vidal A, Canals M,

568   Heussner S, Danovaro R (2016) Organic matter pools, C turnover and meiofaunal

569   biodiversity in the sediments of the western Spitsbergen deep continental margin, Svalbard

570   Archipelago. Deep Sea Research I, 107, 48–58.

571   Ramirez-Llodra E, Ballesteros M, Company JB, Dantart L, Sardà F (2008) Spatio-temporal

572   variations in the diversity biomass and abundance of bathyal invertebrates in the catalan

573   Sea (Western Mediterranean). Marine Biology, 153, 297-309.

574   Rex M, Etter R (1998). Bathymetric patterns of body size: implications for deep-sea

575   biodiversity. Deep-Sea Research II, 45, 103-127

576   Rex MA, Etter RJ, Morris JS, Crouse J, McClain CR, Johnson NA, Stuart CT, Deming JW,

577   Thies R, and Avery R (2006) Global bathymetric patterns of standing stock and body size

578   in the deep-sea benthos. Marine Ecology Progress Series, 317, 1-8.

579   Ricciardi A, Bourget E (1998) Weight-to-weight conversion factors for marine benthic

580   macroinvertebrates. Marine Ecology Progress Series, 163, 245-251.

581   Rogers AD (2015) Environmental Change in the Deep Ocean. Annual Review of

582   Environment and Resources, 40, 1-38.

583   Rowe GT (1983) Biomass and production of deep-sea macrobenthos. In *Deep-sea biology*

584   (Rowe GT editor), New York: Wily-Interscience, 97-121.

585   Rowe GT, Pariente V (1992) *Deep-sea food chains and the global carbon cycle*. Kluwer

586   Academic Publishers: The Netherlands.

587   Rowe GT, Wei C, Nunnally C, *et al.*, (2008) Comparative biomass structure and estimated

588   carbon flow in food webs in the deep Gulf of Mexico. Deep Sea Research Part II, 55 (24–

589   26), 2699-2711.

590   Ruhl HA, Ellena JA, Smith KL (2008) Connections between climate, food limitation, and

591   carbon cycling in abyssal sediment communities. Proceedings of the National Academy of

592   Sciences of the United States of America, 105 (44), 17006–17011.

593   Sanchez-Vidal A, Pasqual C, Kerhervé P, Heussner S, Calafat A, Palanques A, Durrieu de

594   Madron X, Canals M, and Puig P (2009) Across margin export of organic matter by

595   cascading events traced by stable isotopes, northwestern Mediterranean Sea. Limnology

596   and Oceanography, 54(5), 1488–1500.

597 Sardà F, Company JB, Bahamón N, *et al*. (2009) Relationship between environment and the

598   occurrence of the deep-water rose shrimp *Aristeus antennatus* (Risso, 1816) in the Blanes

599   submarine canyon (NW Mediterranean). Progress in Oceanography, 82(4), 227–238.

600 Smith CR, De Leo FC, Bernardino AF, Sweetman AK, Arbizu PM (2008) Abyssal food

601   limitation, ecosystem structure and climate change. Proceedings of the National Academy

602   of Sciences of the United States of America, 23(9), 518-528.

603 Smith KL Jr, Ruhl HA, Bett BJ, Billett DSM, Lampitt RS, Kaufmann RS (2009). Climate,

604   carbon cycling and deep-ocean ecosystems. Proceedings of the National Academy of

605   Sciences of the United States of America, 106(46), 19211-19218.

606 Soltwedel T (2000) Metazoan meiobenthos along continental margins: a review. Progress in

607   Oceanography, 46, 59-84.

608 Soltwedel T, Mokievsky V, Schede I (2000) Benthic activity and biomass on the Yermak

609   Plateau and in adjacent deep-sea regions northwest of Svalbard. Deep-Sea Research I, 47,

610   1761-1785.

611 Stavrakakis S, Chronis G, Tselepides A, Heussner S, Monaco A, Abassi A (2000) Downward

612   fluxes of settling particles in the deep Cretan Sea (NE Mediterranean). Progress in

613   Oceanography, 46, 217–240.

614 Swartz W, Sala E, Tracy S, Watson R, Pauly D (2010) The spatial expansion and ecological

615   footprint of fisheries (1950 to present). PLoS One, 5, e15143.

616 Suttle CA (2007) Marine viruses - major players in the global ecosystem. Nature reviews, 5,

617   801-812.

618   van der Grient JMA, Rogers AD (2015) Body size versus depth: regional and taxonomical

619   variation in deep-sea meio- and macrofaunal organisms. In *Advances in Marine Biology*

620   (BE Curry, editor), Oxford: Academic Press, 71, 71-108

621   van Dover CL (2011) Tighten regulations on deep-sea mining. Nature, 470, 31-33

622   Wei C-L, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T *et al.,* (2010). Global

623   patterns and predictions of seafloor biomass using random forests. Plos One, 5(12),

624   e15323.

625   Wilhelm SW, Suttle CA (1999) Viruses and Nutrient Cycles in the Sea. BioScience, 49(10),

626   781-788.

627   Witte U, Wenzhöfer F, Sommer S, *et al.*, (2003) In situ experimental evidence of the fate of a

628   phytodetritus pulse at the abyssal sea floor. Nature, 424, 763-766.

629   Yasuhara M, Danovaro R (2014) Temperature impacts on deep-sea biodiversity. Biological

630   Reviews doi: 10.1111/brv.12169

631   Yasuhara M, Cronin TM, de Menocal PB, Okahashi H, Linsley BK (2008) Abrupt climate

632   change and collapse of deep-sea ecosystems. Proceedings of the National Academy of

633   Sciences of the United States of America, 105(5), 1556-1560.

634   Zúñiga D, Calafat A, Heussner S, *et al.* (2008) Compositional and temporal evolution of

635   particle fluxes in the open Algero–Balearic basin (Western Mediterranean). Journal of

636   Marine Systems, 70, 196–214.

637

638   Captions of Figures

639   Figure 1. Location of the sampling sites in the deep Mediterranean Sea. The vertical bar

640   represents the bathymetric ranges in meters.

641   Figure 2. Relationships between abundance and depth in the Mediterranean basin. Reported is

642   the abundance ($\log_{10}$ transformed) as a function of depth for viruses, prokaryotes,

643   meiofauna, macrofauna and megafauna (effects of longitude and latitude were removed by

644   partial regression) in a) the whole Mediterranean Sea, b) the Western and c) the Eastern

645   basin.

646   Figure 3. Relationships between biomass and depth in the Mediterranean basin. Reported is

647   the biomass ($\log_{10}$ transformed) as a function of depth for viruses, prokaryotes, meiofauna,

648   macrofauna and megafauna (effects of longitude and latitude were removed by partial

649   regression) in a) the whole Mediterranean Sea, b) the Western and c) the Eastern basin.

650   Figure 4. Relationships between meiofaunal individual biomass and depth in the

651   Mediterranean basin. Reported is the meiofaunal individual biomass ($\log_{10}$ transformed) as

652   a function of depth (effects of longitude and latitude were removed by partial regression) in

653   a) the Western and b) the Eastern basin. Equations are: $y=-9E-05x-3.8$, $p<0.01$ in the

654   Western basin and $y=-0.0003x-2.9$, $p<0.01$ in the Eastern basin.

655   Figure 5. Relative contribution of each benthic component to the total biomass estimated for

656   the selected depth intervals. Data of macrofauna in the depth range 3000-4000m are

657   collected at ca 4300m. Viruses are not visualized in the panel and their contribution ranges

658   from 0.1-0.8% with the increasing of depth.

659   Figure 6. Relationship between meio- and macrofaunal biomass (mgC m^{-2}) and OC fluxes

660   (mgC m^{-2} d^{-1}) in the a) Western and b) Eastern Mediterranean Sea. Equations are: $y=1.7x-$

661   1.2, $p<0.01$ for meiofauna and $y=1.1x-4.2$, $p<0.01$ for macrofauna in the Western basin;

662   y=10.9x-5.4, p<0.01 for meiofauna and y=7.7x+4.3, p<0.01 for macrofauna in the Eastern

663   basin.

664 Figure 7. Ecosystem efficiency in different trophic conditions of the deep Mediterranean Sea.

665   Reported is the ratio between a) total benthic biomass and OC flux (unit y axis: d), b) total

666   benthic biomass and total phytopigments (converted into C equivalents) and c) prokaryotic
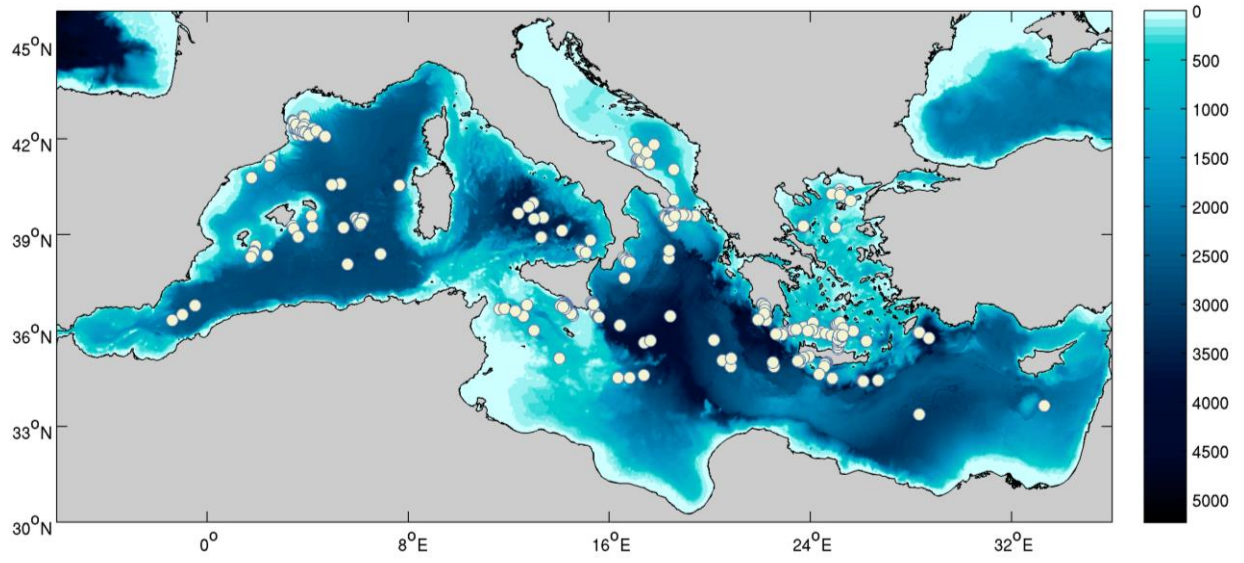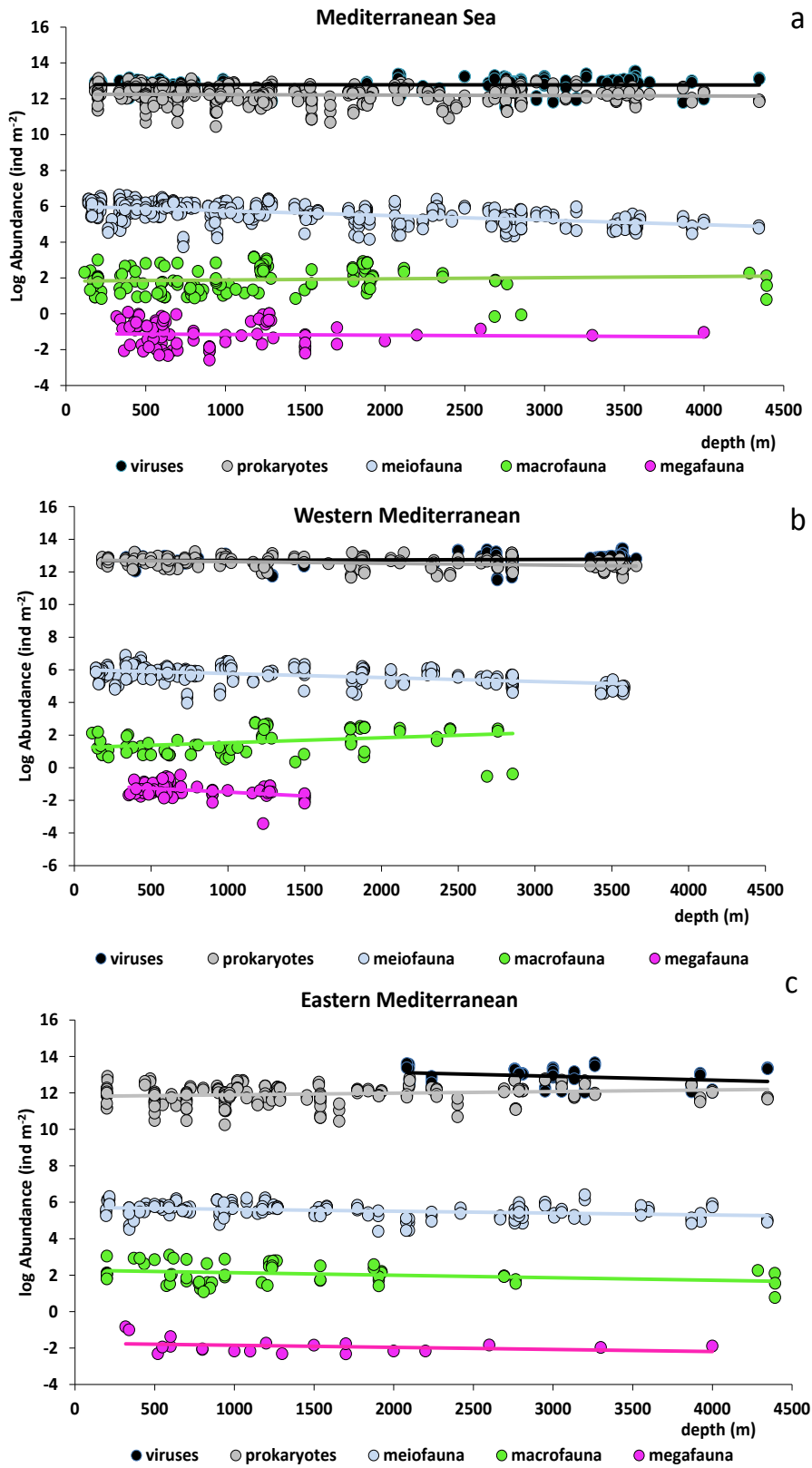
667   biomass and OC flux (unit y axis: d).
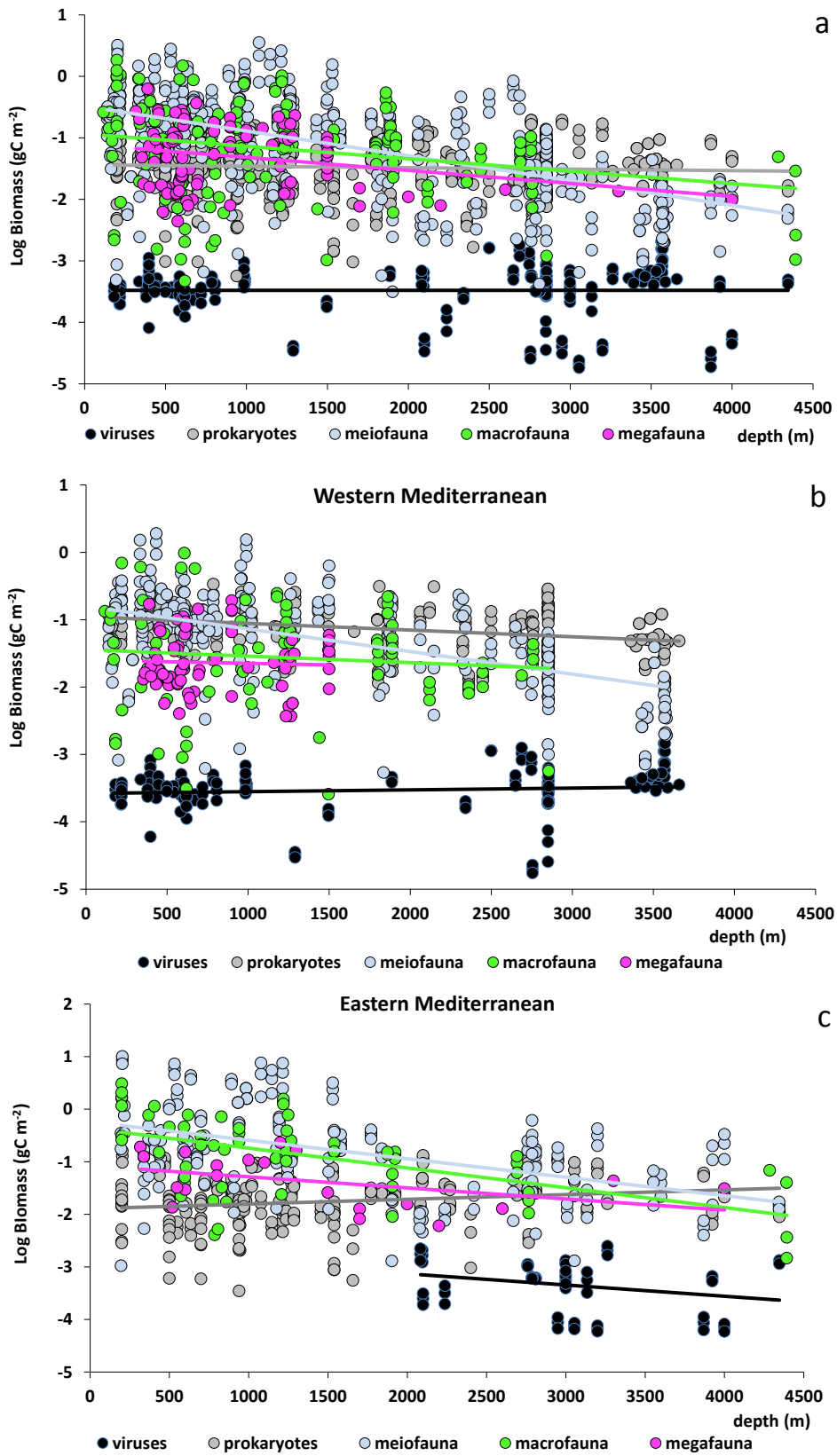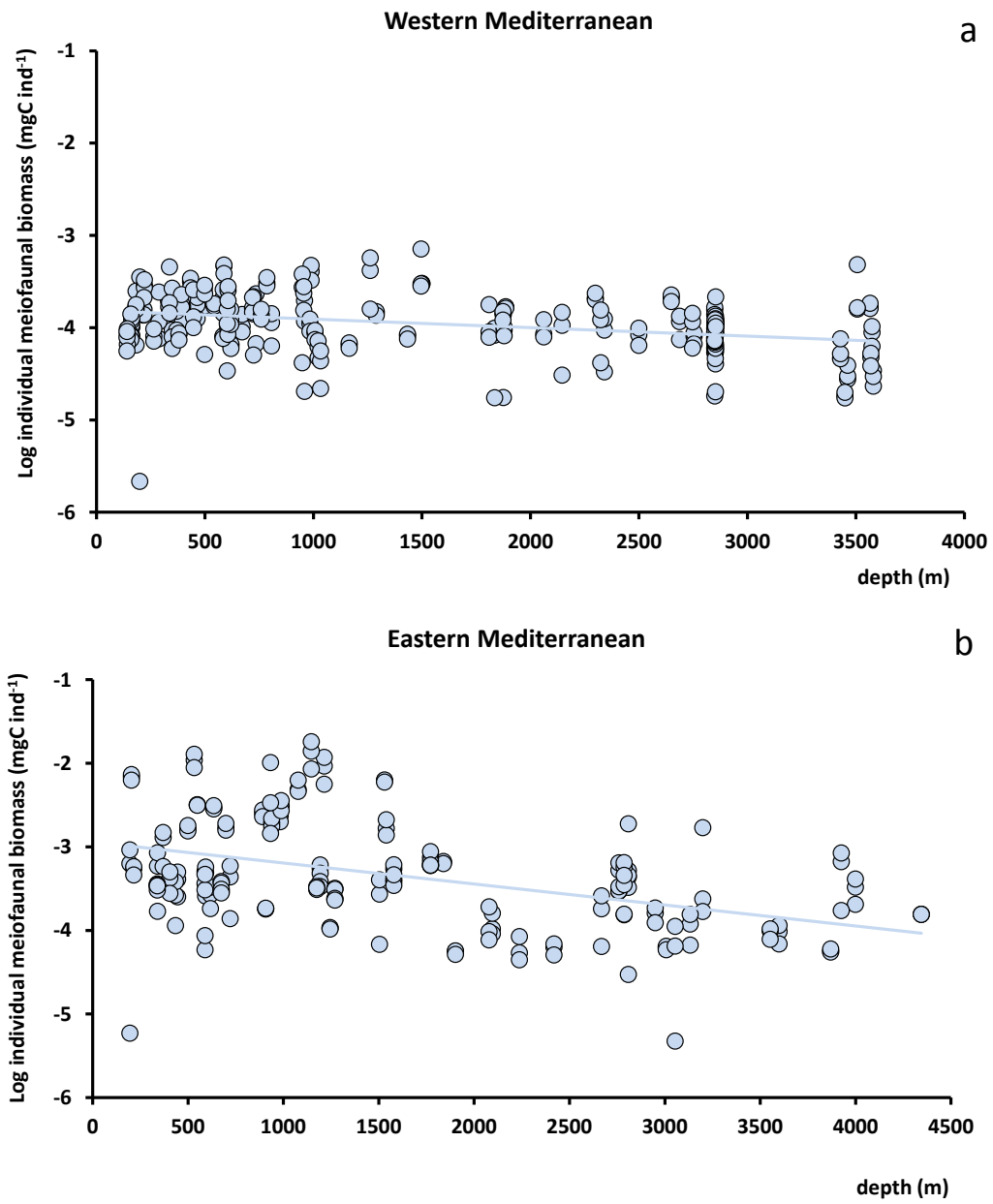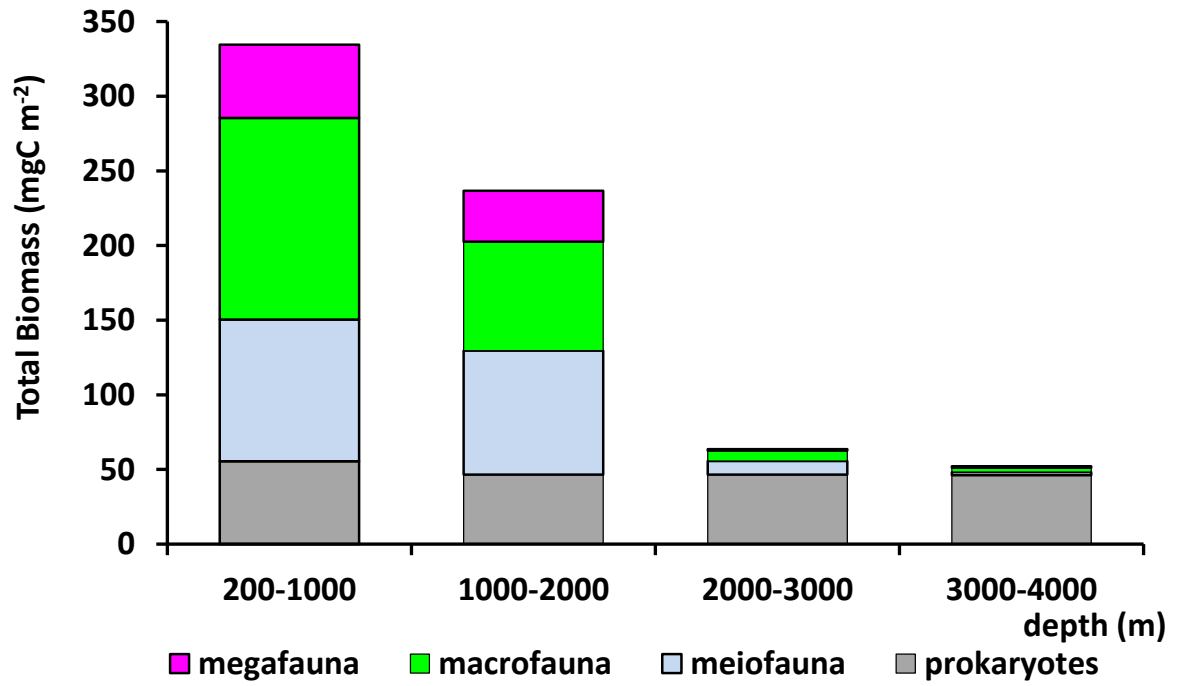
668

669

670

671

672

673

674

675 **Figure 1**

676

677

Figure 2

30

681

Western Mediterranean

Eastern Mediterranean

682

Figure 3

684

Western Mediterranean

Eastern Mediterranean

685
686
687   **Figure 4**
688
689
690

691
692

693
694
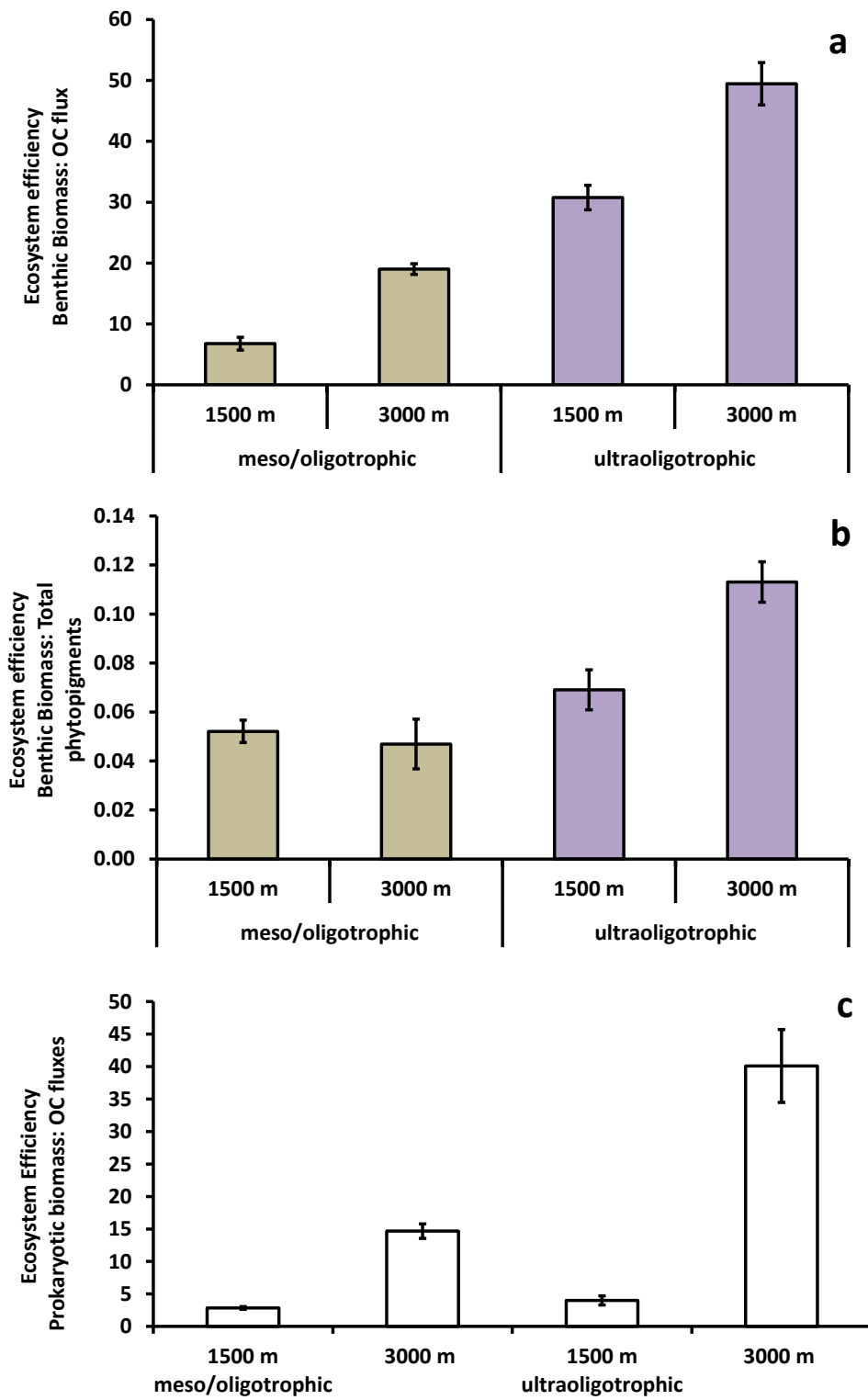695
696 **Figure 5**
697
698

703   **Figure 6**

704

705
706

707
708
709 **Figure 7**
710
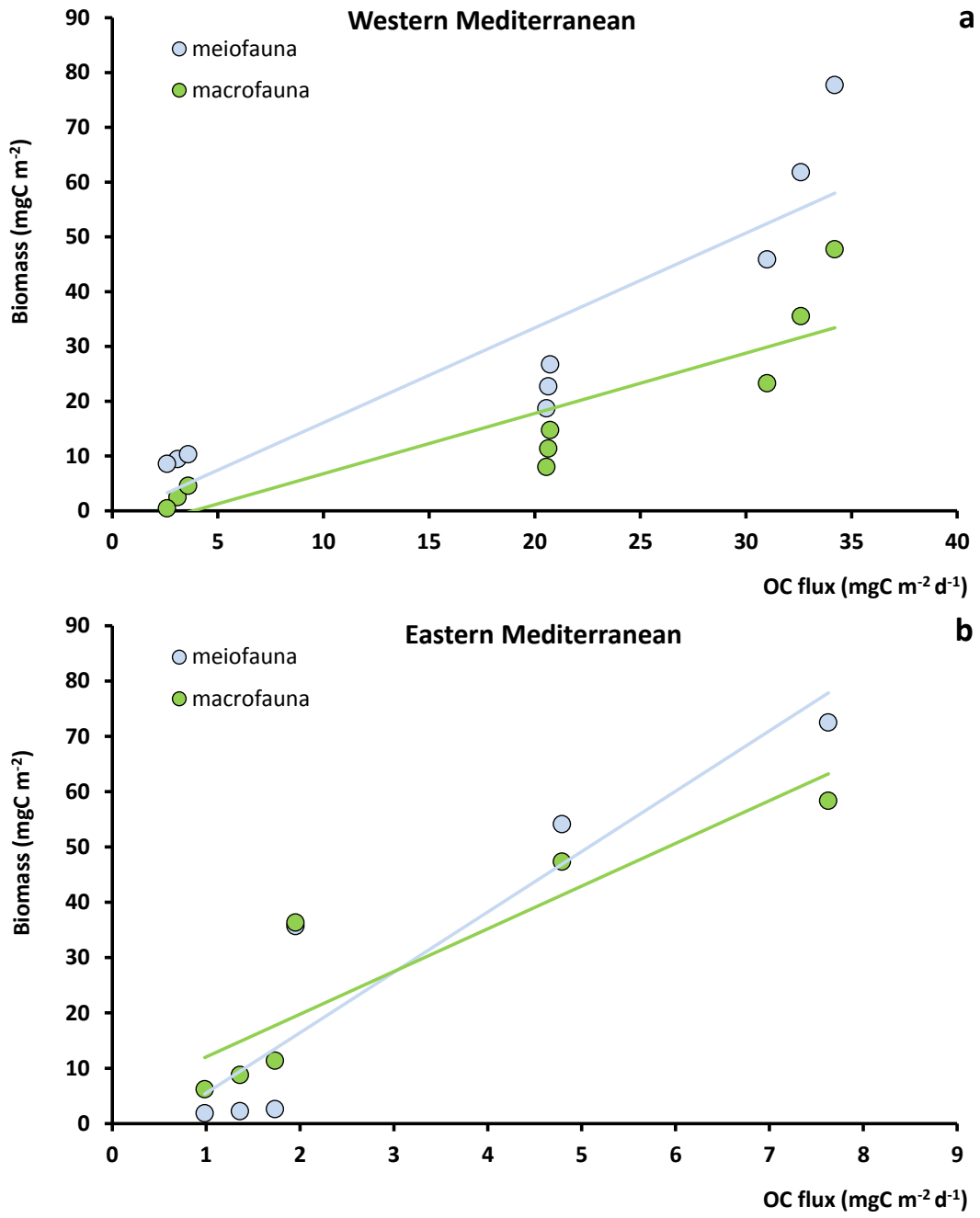
711 **Table 1**. Regression analyses of benthic abundance and biomass against depth for viruses,
712 prokaryotes, meiofauna, macrofauna and megafauna. Response variable are Log_{10} transformed,
713 predictor is depth (m). Scatter plots of the response variables against predictor and regression lines are
714 in Figures 2 and 3. N: num. samples; *=$P<0.05$; **=$P<0.01$; ***=$P<0.001$; ns: not significant.

Regression	Equation	N	P
Log_{10} Abundance (ind m^{-2})			
Mediterranean Sea			
Viruses	y = 12.8 - 7E-06x	265	ns
Prokaryotes	y = 12.3 - 0.00003x	508	ns
Meiofauna	y = 6.0 - 0.0003x	501	***
Macrofauna	y = 1.8 + 0.00005x	143	ns
Megafauna	y = - 1.1 - 0.00004x	92	ns
Western basin			
Viruses	y = 12.7 - 0.0003x	199	ns
Prokaryotes	y = 12.7 - 0.0001x	265	***
Meiofauna	y = 6.0 - 0.0002x	297	***
Macrofauna	y = 1.2 + 0.0003x	80	***
Megafauna	y = - 1.0 - 0.0005x	72	***
Eastern basin			
Viruses	y = 13.6 - 0.0002x	66	*
Prokaryotes	y = 11.8 + 9E-05x	243	***
Meiofauna	y = 5.7 - 0.0001x	204	***
Macrofauna	y = 2.3 - 0.0001x	63	*
Megafauna	y = - 1.7 - 0.0001x	20	ns
Log_{10} Biomass (gC m^{-2})			
Mediterranean Sea			
Viruses	y = - 3.5 - 1E-17x	265	ns
Prokaryotes	y = - 1.4 - 0.00002x	508	ns
Meiofauna	y = - 0.5 - 0.0004x	501	***
Macrofauna	y = - 0.9 - 0.0002x	143	**
Megafauna	y = - 1.1 - 0.0002x	92	*
Western basin			
Viruses	y = - 3.6 - 0.00003x	199	ns
Prokaryotes	y = - 1.0 - 0.0001x	265	***
Meiofauna	y = - 0.8 - 0.0003x	297	***
Macrofauna	y = - 1.4 - 0.0001x	80	ns
Megafauna	y = - 1.6 - 0.00005x	72	ns
Eastern basin			
Viruses	y = - 2.7 - 0.0002x	66	*
Prokaryotes	y = - 1.9 + 0.00009x	243	**
Meiofauna	y = - 0.2 - 0.0004x	204	***
Macrofauna	y = - 0.4 - 0.0004x	63	***
Megafauna	y = - 1.1 - 0.0002x	20	ns

715

716

717 **Biosketch**

718 The Marine Biology and Ecology research team of the Department of Life and Environmental

719 Sciences of the Polytechnic University of Marche include a highly interdisciplinary and

720 multidisciplinary group of scientists who are devoted to the investigation of marine biology

721 and ecology, with a special focus on the understanding of the links between biodiversity and

722 ecosystem functioning, and of the management and protection of deep-sea habitats.

723

724 **Cristina Gambi** works in the Department of Life and Environmental Sciences of the

725 Polytechnic University of Marche, in Italy. Her research interests are focused on deep-sea

726 ecology, with a special focus on the understanding of the patterns of biodiversity at large

727 spatial scales, and of the relationships between biodiversity and ecosystem functioning in

728 deep-sea ecosystems.

729