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1 **Insights into biotic and abiotic modulation of ocean mesopelagic communities**

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50 Running title: Mesopelagic community ecology
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54

55 **Abstract**

56

57 Marine plankton mitigate anthropogenic greenhouse gases, modulate biogeochemical cycles,
58 and provide fishery resources. Plankton is distributed across a stratified ecosystem of sunlit
59 surface waters and a vast, though understudied, mesopelagic 'dark ocean'. In this study, we
60 mapped viruses, prokaryotes, and pico-eukaryotes across 32 globally-distributed cross-depth
61 samples collected during the *Tara* Oceans Expedition, and assessed their ecologies. Based
62 on depth and O₂ measurements, we divided the marine habitat into epipelagic, oxic
63 mesopelagic, and oxygen minimum zone (OMZ) eco-regions. We identified specific
64 communities associated with each marine habitat, and pinpoint environmental drivers of dark
65 ocean communities. Our results indicate that water masses primarily control mesopelagic
66 community composition. Through co-occurrence network inference and analysis, we identified
67 signature communities strongly associated with OMZ eco-regions. Mesopelagic communities
68 appear to be constrained by a combination of factors compared to epipelagic communities.
69 Thus, variations in a given abiotic factor may cause different responses in sunlit and dark
70 ocean communities. This study expands our knowledge about the ecology of planktonic
71 organisms inhabiting the mesopelagic zone.

72

73 **Keywords:** mesopelagic community, metabarcoding, plankton, pan-oceanic expedition,
74 oxygen minimum zone

75

76 **Introduction**

77

78 Below the ocean's sunlit layer lies the mesopelagic zone that occupies around 20% of the

79 global ocean volume [1]. The mesopelagic zone is biologically defined as starting where

80 photosynthesis no longer occurs (<1% irradiance around 200m depth), down to its lower

81 boundary where there is no detectable sunlight (around 1000m depth) [2]. This twilight

82 ecosystem cannot rely on photoautotrophy, but sustains its energetic requirements by the

83 combination of heterotrophic, chemoautotrophic, and chemo-mixotrophic metabolisms,

84 together with physicochemical processes. Among the latter, the fraction of upper ocean

85 productivity that escapes epipelagic recycling and sinks by gravity or is delivered by the daily

86 migration of zooplankton constitutes an essential energy source in deep waters and is a vector

87 for attached organisms [3].

88 The biodiversity and biomass in mesopelagic communities have been underestimated in the

89 past [2, 4], and previous work showed these communities hold an enormous unexploited

90 biological resource [5, 6, 1]. Mesopelagic organisms are considered to be a vast source of fat

91 and protein, potentially becoming the primary source of global bioeconomy [7]. So far, efforts

92 have been made to increase knowledge of mesopelagic mega/macrofauna by studying the

93 abundance and diversity of nekton. These efforts are of great importance, given the rapid

94 increase in the exploitation of this zone by nutraceutical and fisheries industries [6]. However,

95 less attention has been devoted to the mesopelagic community's microscopic fraction, despite

96 the pivotal role of the marine microbiome in biogeochemical cycles. The marine microbiome

97 makes crucial links in the food web between primary production and dark ocean specialized

98 consumers. Previous reports have shown stratification of planktonic communities with depth.

99 In this regard, the mesopelagic zone displays a distinct assemblage of dsDNA viruses [8], giant

100 viruses [9], prokaryotes [10, 11], and eukaryotes [12]. However, unlike the epipelagic layer,

101 mesopelagic plankton diversity does not show the latitudinal diversity gradient trends from

102 pole-to-pole, peaking at lower latitudes [13].

103 Among the studies conducted in mesopelagic zones, we highlight the efforts to explore regions

104 of extreme conditions, such as oxygen minimum zones (OMZs). These zones are formed by

105 relatively old slowly upwelling waters, often lying below highly productive surface zones [14],
106 and are currently increasing in volume in the oceans [15]. OMZ prokaryotic communities are
107 well documented and predominated by taxa such as Nitrospira, Marinimicrobia, and anammox
108 bacteria from the phylum Planctomycetes, while Thaumarchaeota abundance is frequently
109 lower in these zones [16, 17, 18, 19, 20]. In contrast, knowledge of eukaryotic diversity in OMZs
110 is still rudimentary, but a prevalence of specific taxa such as Ciliophora, Dinoflagellata, MALV,
111 and Acantharia has been reported, together with a higher metabolic activity of these taxa [21,
112 22, 23]. Understanding plankton community structure and dynamics is fundamental to
113 anticipate the impacts of global warming and acidification in these regions.

114 The last decades have seen a significant increase in large-scale oceanic surveys [24, 25, 26].
115 However, most mesopelagic community studies have been limited to geographically or
116 ecologically fragmented regions, or to specific taxonomic groups, mainly because of the
117 inherent difficulties of accessing this zone on a global scale [5]. Hence, these studies have
118 given us a limited picture of community composition. Moreover, the factors influencing
119 community structure, presumably a combination of biotic and abiotic factors [27, 28], have
120 been little explored in the mesopelagic zone.

121 The present study takes advantage of the *Tara* Oceans large-scale survey conducted in
122 different water layers using a systematic sampling protocol, spanning viruses to small
123 eukaryote size fractions, to investigate the mesopelagic biome [29]. We capitalized on genomic
124 data together with extensive contextual data and ocean geography to explore the particularities
125 of mesopelagic communities compared to communities found in the euphotic zone. We also
126 investigated potential water deoxygenation effects on these communities by comparing OMZ
127 communities with those from well-oxygenated waters. This work expands our knowledge of
128 the web of relationships underpinning mesopelagic plankton ecosystems on a broad
129 geographic scale.

130

131 **Materials and Methods**

132 **• Sample collection and pre-processing**

133 The environmental and biological data were obtained during the *Tara* Oceans expedition
134 (2009- 2012) in 32 oceanographic stations located in the Indian Ocean (IO - 037, 038, 039),
135 Pacific Ocean (PO - 097, 098, 100, 102, 106, 109, 110, 111, 112, 122, 131, 132, 133, 135,
136 137, 138), South Atlantic Ocean (SAO - 068, 070, 072, 076, 078) and North Atlantic Ocean
137 (NAO - 142, 143, 144, 145, 146, 148, 149, 152) comprising tropical and subtropical regions
138 (Figure 1). Physico-chemical environmental data were obtained along a vertical profile at each
139 station. Temperature, salinity, and oxygen were measured using a CTD-rosette system with a
140 coupled dissolved oxygen sensor. Chlorophyll-a concentrations were measured using high-
141 performance liquid chromatography. Nutrient concentrations were determined using
142 segmented flow analysis. Metadata are available at PANGAEA [30, 31, 32, 33, 34, 35] -
143 (<https://doi.pangaea.de/10.1594/PANGAEA.875582>).

144 The vertical distribution of marine particles was investigated with an Underwater Vision Profiler
145 (UVP, [36, 37]) mounted on the CTD-Rosette. The UVP acquires images in a coherent water
146 volume (1 L) delimited by a light sheet issued from red light-emitting diodes. Automatic
147 identification of objects was made using Ecotaxa, based on a learning set of visually identified,
148 manually classified objects and associated features. Images were classified to distinguish
149 mesozooplankton from non-living objects and artifacts (e.g., detritic particles, fibers, and out-
150 of-focus objects).

151 Water vertical profiles of temperature and salinity generated from the CTD were used to identify
152 the water masses by plotting a temperature x salinity (T/S) diagram using the Ocean Data View
153 V 5.0 (ODV) software package [38].

154 Three different water layers were sampled: surface (SRF, 3-7 m), deep chlorophyll maximum
155 (DCM - depth identified according to the peak of chlorophyll-a fluorescence obtained *in situ*),
156 and mesopelagic (ranging from 200-1000 m) [39]. The planktonic community was sampled by
157 partitioning the seawater by filtering each sampled depth with different filter sizes [34]. Among
158 the mesopelagic zones, 13 of them were identified as deficient in oxygen and classified as

159 oxygen minimum zone (OMZ, stations IO - 037, 038, 039 / PO - 100, 102, 106, 109, 110, 111,
160 133, 135, 137, 138). The OMZ were categorized as suboxic: $<10 \mu\text{M O}_2/\text{kg}$ seawater and
161 anoxic: ($<0.003 \mu\text{M}/\text{kg}$ seawater or undetectable with most sensitive techniques, e.g., STOX
162 sensors) [Units of O_2 concentration: $1 \text{ mL}\cdot\text{L}^{-1}=1.43 \text{ mg}\cdot\text{L}^{-1}=44.64 \mu\text{M}$] [22].

163 Our dataset comprises different organismal size-fractions from viruses (two dsDNA-virus
164 families *Podoviridae* and *Myoviridae* - hereafter named as phages and NCDLV giant viruses -
165 hereafter named as giruses) to pico-eukaryotes. Phage libraries were constructed from
166 seawater samples filtered at $0.22 \mu\text{m}$, concentrated using iron chloride flocculation, and treated
167 with deoxyribonuclease (DNase). Girus *polB* and prokaryotic 16S rDNA sequences were
168 extracted from plankton metagenomes sequenced from $0.22\text{--}1.6$ or $0.22\text{--}3 \mu\text{m}$ filters, and the
169 pico-eukaryote dataset was obtained by V9-18S rDNA marker amplification from $0.8\text{--}3$ or 0.8--
170 $5 \mu\text{m}$ filters. Details of sample preparation and sequencing procedures are described in Alberti
171 et al. [40].

172 Phage relative abundance was accessed through the search for the marker genes *gp23*
173 (*Myoviridae*) and *polA* (*Podoviridae*) in the protein collection GOV2.0 derived from
174 metagenomic sequencing described in Gregory et al. [8]. The girus abundance profile was
175 obtained from *polB* marker gene gathered from the OM-RGC.v2 catalog [11] as described in
176 Endo et al. [9]. The Prokaryote 16S rDNA marker derived from the metagenome assembly,
177 named 16S Mitag, is described in Sunagawa et al. [10]. Sequences matching “Eukaryota”,
178 “chloroplasts”, and “mitochondria” were removed from the final table. Clustering and annotation
179 of pico-eukaryote V9-18S rDNA amplicons are described in de Vargas et al. [41], and functional
180 annotation of taxonomically assigned V9-18S rDNA metabarcodes was improved afterward; in
181 this case, we conserved in the final data only sequences assigned to the “Eukaryota” domain.

182 We concatenated SRF and DCM samples for each taxonomic group to obtain an epipelagic
183 dataset (EPI). Counts of OTUs shared in SRF and DCM samples were summed. OTU
184 abundance was normalized by the total counts for each taxonomic group within each sample.

185

186 • **Ecological Analysis**

187 **Epipelagic and Mesopelagic Community and Environmental differences**

188 We applied an NMDS analysis based on the Bray-Curtis dissimilarity matrix on relative
189 abundances using the ‘metaNMDS’ function from the vegan R package [42] to confirm
190 community differences between epipelagic and mesopelagic layers. Homogeneity of the
191 sampled environmental parameters was checked using the ‘betadisper’ function (Homogeneity
192 of multivariate dispersions in the vegan package). The analysis was conducted using the
193 Euclidean distance matrix of the environmental variables using the depths (epipelagic,
194 mesopelagic) as group factor. A permutation test statistically confirmed the results.

195

196 **Ecological model selection**

197 We used the Species Abundance (SAD) and Rank Abundance Distribution curves (RAD: log
198 abundances vs. rank order) to fit some of the most popular ecological models assessing how
199 communities are assembled [43, 44]. Niche/deterministic models presume that the community
200 is under selection due to biotic and abiotic interactions, while neutral/stochastic models
201 assume that random processes structure the community such as drift, migration, birth, and
202 death [45, 46]. SAD is essential for describing and understanding community assemblage and
203 its management [44]. Further, by showing logarithmic species abundance against a rank order,
204 RAD is commonly used to investigate a community’s structure from observations made at one
205 point in space and time [43, 44]. All the abundance distributions were fitted using ‘fitsad’ (sads
206 R package - [47]), and ‘radfit’ (vegan) functions using maximum likelihood estimation. A set of
207 candidate models was selected *a priori* to be tested by SAD: Log-series, Poisson-lognormal,
208 Broken Stick, Power Law, and the neutral ecological model Zero-sum multinomial distribution.
209 The neutral ecological model describes the SAD of a sample taken from a neutral
210 metacommunity under random drift. The models selected to be tested by RAD were niche pre-
211 emption models (geometric series or Motomura model), lognormal, Zipf, and Zipf–Mandelbrot,

212 and the null model that infers that the individuals are randomly distributed among observed
213 species. For a complete description of each model see Magurran and McGill [48].

214 The Akaike's Information Criterion (AIC) was used to evaluate the fitted model's quality based
215 on log-likelihood penalized by the number of estimated parameters. AIC estimates the loss of
216 information if the model is assumed for a given dataset. In this manner, models with lower AIC
217 values are selected as better fit conditions [49]. The AIC values produced for each model were
218 compared using the delta AIC (Δ_i). A Δ_i value <2 indicates equally likely models, values $3 < \Delta_i$
219 <9 indicate less likely models, and $\Delta_i > 10$ for no likely models [49].

220

221 **Ecological inferences and statistics**

222 Ecological patterns were inferred using environmental variables to constrain the variation
223 observed in biological data for planktonic samples using Canonical Correspondence Analysis
224 (CCA) in the vegan R package. A set of physico-chemical variables for the discrete depths
225 were selected for the ecological inferences, such as nitrate (NO_3^-), oxygen, temperature,
226 salinity, density, and particles using particle flux UVP data. In order to avoid collinearity among
227 factors, the selected variables were checked for variance inflation factor using the `vif.cca`
228 function and tested for significance by 'anova' implemented in vegan with 999 permutations.
229 Each variable effect significance was tested individually using all the others as covariables
230 (independently from their order in the model) by applying the option 'margin' to the 'anova'
231 function in vegan.

232 Permutational multivariate analysis of variance (PERMANOVA) was performed with the
233 function 'adonis' in vegan to determine the relationship between mesopelagic community
234 composition and predefined water masses based on 999 permutations.

235

236 **Organism Eco-region classification**

237 In order to detect organisms specific to epipelagic (EPI), oxic mesopelagic (Oxic MES), and
238 OMZ eco-regions, only data containing both epipelagic and mesopelagic information were

239 considered: in total, 25 stations for giruses, prokaryotes, and pico-eukaryotes, and 13 for
240 phages. First, we discarded OTUs with fewer than 100 reads to remove biases due to rare
241 species' presence, and then recalculated the relative abundances for each dataset. Next, we
242 ran a Kruskal-Wallis test ('kruskal.test' from stats R package [50]) to detect differential OTU
243 relative abundances between eco-regions, followed by a Bonferroni correction to avoid Type I
244 error. Organisms with a p-value <0.05, indicating a difference within groups, were subject to a
245 post-hoc Dunn test ('dunn.test' from dunn.test R package [51]) to identify preferential Eco-
246 regions for each OTU. From these results, OTUs statistically equally abundant in all Eco-
247 regions or non-significant Kruskal-Wallis tests were assigned to the "ubiquitous" group. In
248 contrast, those with significant p-values were classified as EPI, Oxidic MES, or OMZ if only the
249 corresponding Eco-region was elected according to the Dunn test. Organisms with no
250 significant differences between Oxidic MES and OMZ were assigned to Core MES.

251

252 **Co-occurrence Network**

253 For investigation of associations between organisms across Eco-regions, a co-occurrence
254 network was inferred. In this analysis, phage samples were not included due to the lower
255 number of stations sampled. Therefore, samples for giruses, prokaryotes and pico-eukaryotes
256 from stations 038, 039, 068, 070, 072, 076, 078, 098, 100, 102, 109, 110, 111, 112, 122, 132,
257 133, 137, 138, 142, 145, 146, 148, 149 and 152 were retained. OTUs with a relative abundance
258 10^{-4} and counting fewer than 5 observations were discarded. Next, each sample was
259 normalized by applying a centered-log-ratio (CLR) transformation. Network inferences were
260 performed using Flashweave version 0.18 developed in Julia version 1.2 [52], using the
261 sensitive and heterogeneous mode.

262 We analyzed this global co-occurrence network by delineating communities (or modules) using
263 the Clauset-Newman-Moore algorithm [53]. These modules are subsets of OTUs, obtained by
264 maximizing the co-occurrences within the module and minimizing connections between them.
265 Next, we investigated modules enriched in OTUs from specific Eco-regions using Fisher's
266 exact test using the "fisher.test" function from the stats R package.

267

268 **Results and Discussion**

269

270 Leveraging the resources produced by the *Tara* Oceans project, we deciphered differences
271 between epipelagic and mesopelagic beta-diversity stratification, with a particular emphasis
272 on the role of environmental variables such as temperature, oxygen, salinity, NO_3^- , chlorophyll-
273 a, and particle flux (see Methods). As previously reported, we observed a stratification by depth
274 of the epipelagic and the mesopelagic communities (i.e., phages, giruses, prokaryotes, and
275 pico-eukaryotes) (Supplementary Figure 1). Consequently, we investigated differences among
276 epipelagic and mesopelagic sampling sites based on Euclidean distance of physicochemical
277 characteristics from each site. We observed a high dissimilarity gradient among sites for both
278 layers (Supplementary Figure 2a, b). Mesopelagic samples were spread in the plot, with most
279 of the points placed distant from the group centroid (located in the center of the cloud of points
280 identified for each group) (Supplementary Figure 2a). In contrast, epipelagic points displayed
281 a large variance due to a few samples positioned apart from the main cluster (Supplementary
282 Figure 2a). These results probably underlie the heterogeneity of environmental conditions
283 encountered in both sampled layers, and this environmental variation may be an important
284 factor that can directly influence community composition.

285 Community composition variations can also be shaped by four main eco-evolutionary
286 processes: selection, dispersal, drift, and speciation [54]. Mathematical models based on these
287 processes and applied to species abundance (SAD) and rank abundance (RAD) distributions
288 are historically used to infer the ecological or evolutionary mechanisms that structure a given
289 community [55]. Here, we addressed these biological processes to infer the abundance
290 distributions as observed in such natural communities [56, 57] in the most diverse
291 environments (terrestrial and aquatic) [45, 46, 43]. We used both SAD and RAD as evidence
292 of ecological processes related to variations in plankton community composition. When applied
293 at the local scale, we excluded random/neutral evolutive effects because all epipelagic and

294 mesopelagic communities fit the niche/deterministic ecological models. In fact, in all cases, we
295 found a Δ_i value <2 for both methods evaluated, which allows us to select one best-fitting model
296 without a subjective judgment (Supplementary Material Table 1 and 2) [49]. In these cases,
297 the community assemblages are mediated by a combination of environmental conditions,
298 interspecies interactions (competition, predation, or mutualisms), and species traits (for
299 instance, phototrophy, parasitism). Specifically, 93% and 65% of epipelagic and mesopelagic
300 samples better fit the Lognormal model (Poisson Lognormal SAD [58] and Lognormal RAD
301 [59]), respectively). These results suggest that EPI and MESO plankton populations are
302 affected by the combination of many independent variables, including competitive biotic
303 interactions and abiotic factors [43]. According to this model, the community has a broad and
304 elementary form of organization [57]. Ser-Giacomi et al. [60] stated that the eukaryotic rare-
305 biosphere (non-dominant OTU's) composed of "transient" or occasional taxa in the ocean sunlit
306 layer are mainly governed by dispersal/neutral events. In contrast, and in the case of our
307 findings, the dominant fraction of the assemblage follows idiosyncratic environmental
308 conditions.

309 Next, to quantify how much of the differences in the assemblages' variance can be explained
310 by environmental conditions, we employed canonical correspondence analysis (CCA) using
311 the environmental variables measured at discrete depths as constraint variables. The results
312 showed that the environment explains only a small fraction of community variance for both
313 layers (32% on average) (Figure 2). The phage assemblage was the exception, for which about
314 55% of the epipelagic variation and 65% of the mesopelagic variation could be explained by
315 the variables investigated (Figure 2). We tested the variance explained by single explanatory
316 variables individually. In contrast with epipelagic communities mainly governed by temperature
317 and oxygen, as observed here and elsewhere [10, 61, 8, 13, 12, 62], we could not identify a
318 single environmental predictor structuring entire mesopelagic assemblages. However, a few
319 different variables appeared to be significant for each group (Table 1, complete analysis in
320 Supplementary Material Table 3). Notably, our analysis identified oxygen as the main

321 mesopelagic driver for phage and prokaryote assemblages, confirming previous reports [20,
322 63, 64].

323 Even though we observed in the ordination-plots the distinction of OMZ and oxic mesopelagic
324 (Oxic MES) stations for viruses and pico-eukaryote assemblages (Figure 2, diamond and down
325 triangle), we could not disentangle the effect of oxygen from the other variables included in the
326 analyses (Table 1, complete analysis in Supplementary Material Table 3). This result shows
327 that these assemblages are probably affected by a combination of the predictors evaluated,
328 reflecting their need to cope with a broader environmental gradient that maximizes their niche-
329 space partitioning. Previous studies have identified oxygen as one of the main drivers of the
330 eukaryotic community structure in OMZ regions [65, 22, 23]. These studies mainly compared
331 community composition along the oxygen gradient within the water column depth, from the
332 surface downwards. However, depth stratification of plankton communities is evident even in
333 regions with high oxygen concentrations, so distinct parameters co-varying with depth must be
334 taken into account in addition to the oxygen gradients [66].

335 In addition to the physicochemical parameters, our results show that particle flux derived from
336 UVP measurements was also a significant variable structuring the phage assemblages in both
337 epipelagic and mesopelagic layers (Table 1, complete analysis in Supplementary Material
338 Table 3). This data supports previous reports about the high correlation of this environmental
339 factor with phages, finding possible relevance for the carbon pump's functioning in epipelagic
340 layers [67]. This observation may also reflect the association with virus inputs from overlaying
341 water layers via sinking particles [68].

342 *In situ* physico-chemical measurements have revealed the dynamics and fluctuating nature of
343 the ocean, even at short time scale [69]. The heterogeneity in mesopelagic layers given by
344 deep currents, and by the impact of the surface production, together with the low mixing levels,
345 may favor a diversification in the mesopelagic community living in different water masses,
346 leading to species adaptation-acclimation. The *Tara* Oceans expedition route included

347 samples from common or distinct water masses defined by temperature/salinity profiles - T/S,
348 comprising regionally connected or unconnected stations. We identified nine different water
349 masses in the mesopelagic sampled locations (Figure 3). We could confirm significant
350 differences in mesopelagic communities sampled in different water masses based on the
351 PERMANOVA test (Table 2). This result indicates that the oceanic patchiness created by
352 distinct water masses can favor beta-diversity diversification, indicating it to be a critical
353 component for mesopelagic community variation for all the assemblages studied (phages,
354 giruses, prokaryotes, and pico-eukaryotes). Thus, we hypothesize that this result may be
355 explained by two non-exclusive causes related to water masses: (i) past common origin among
356 water masses that have drifted or (ii) constant connectivity by ocean circulation between
357 sampled sites belonging to the same water mass.

358 Following the biotic control suggested by the deterministic model previously identified, we
359 addressed another lingering question, resolving planktonic community signatures of Oxic MES
360 and OMZ regions for epipelagic communities. For this, we classified OTUs based on their
361 relative abundance into three eco-regions: 1) EPI, 2) Oxic MES, and 3) OMZ. OTUs were
362 classified as Core MES when commonly present in Oxic MES and OMZ samples. The taxa
363 that were either equally abundant in all three eco-regions or not statistically confirmed to a
364 single eco-region were classified as ubiquitous (Supplementary Figure 3). Using this approach,
365 we could identify ubiquitous taxa, that are likely to thrive in a wide range of environmental
366 conditions, or that may be detected in mesopelagic samples due to the simple vertical
367 movement of sinking particles. This classification should help avoid putative biases inherent of
368 the metabarcoding methodology.

369 More specifically, we were able to identify Oxic MES and OMZ signatures mainly at the infra-
370 taxonomic level (OTU-species) for all biotic groups investigated (Figure 4, Supplementary
371 Figure 3, 4, 5, 6, 7). This reflected the wide ecological niche occupied by the different species
372 at a higher taxonomic level (i.e. family). At the species level, we observed large taxonomic
373 plasticity of OTUs that occurred equally in both Oxic MES and OMZ samples, called Core MES,

374 principally for girus assemblages. However, most OTUs are not yet classified at the infra-
375 taxonomic level (data not shown). This observation reflects the knowledge gap about the
376 biodiversity and functional plasticity of species thriving in this ecosystem.

377 The great majority of phage taxa occurred at similar abundance in all regions (ubiquitous)
378 (Supplementary Figure 3, 4). Surprisingly, this ubiquity is vertically linked at each independent
379 station (Supplementary Figure 4), supporting the seed-bank hypothesis raised by Brum et al.
380 [60], and the correlation to the sinking particles observed here. We observed taxa specific to
381 the mesopelagic layer in second place, mostly related to the OMZ eco-region (Figure 4a,
382 Supplementary Figures 3, 8). This mesopelagic specificity agrees with the sharp increase in
383 marine phage microdiversity following depth, as previously shown by Gregory et al. [8]. Our
384 results emphasize that one cause for phage stratification in the water column might be the
385 adaptation to the mesopelagic environment. Two hypotheses arise here, 1) the environment
386 acts as a strong driver, directly selecting phages independently of their hosts, and 2) there is
387 higher phage-host specificity in the mesopelagic layer, promoting phage selection. Following
388 the first hypothesis, we can posit that the environment can directly impact phage assemblage
389 composition. The direct contact with the environment of free phage particles (released from
390 their hosts) may reduce infectivity, degrade, or remove virus particles, and adversely affect
391 adsorption to the host [70]. This direct environmental effect over marine phages was reported
392 for different ionic gradients [71], daylight conditions, and temperature [72]. However, the
393 enrichment of prokaryotic OTUs specific to mesopelagic regions (Supplementary Figures 3,
394 8), especially in OMZs, does not exclude the phage-host indirect selection relationship.

395 We found fewer but abundant mesopelagic-specific girus OTUs in both Oxic and OMZ eco-
396 regions, indicating that giruses can be less diverse in the mesopelagic layer (Figure 4b,
397 Supplementary Figures 5, 3, 8). Also, giruses can encode genes such as transporters for
398 ammonium, magnesium, and phosphate that are important in marine oligotrophic areas [73].
399 This characteristic can improve the host's fitness in the short-term but ultimately favor girus
400 fecundity and endurance. This property is named NCLDV-mediated host reprogramming [73].

401 The great majority of mesopelagic girus OTUs were assigned to the Core MES group,
402 indicating that these entities may infect a wide range of hosts adapted to diverse environmental
403 conditions.

404 We could better distinguish the prokaryotic mesopelagic signatures between Oxic MES and
405 OMZ, confirming the influence of oxygen reported here and in previous studies [18, 19, 20]
406 (Figure 4c, Supplementary Figures 6, 3, 8). Among the planktonic microorganisms,
407 prokaryotes have been, so far, the most investigated group in OMZ regions, especially in the
408 Pacific Ocean [60, 19, 18]. We observed similar occurrence and abundance for the OMZ
409 signature taxa in the Indian Ocean stations (IO - 037, 038, 039) and in stations PO - 100, 137,
410 and 138 from the Pacific Ocean (Figure 4c). These Pacific stations are located in the open
411 ocean (PO - 137 and 138 located in the Equatorial upwelling zone and station PO - 100 in the
412 South Pacific Subtropical Gyre). They present a strong upwelling signature, disclosing an
413 intense decrease in oxygen concentration almost reaching shallow waters. Likewise, the
414 sampling stations in the Indian Ocean are located in well-stratified waters, markedly
415 characterized by the abrupt decrease of oxygen concentration below the thermohaline at 100-
416 120m depth. In all these stations, the oxygen concentration ranges from 0.83 to 3 $\mu\text{mol/kg}$,
417 characterizing functionally anoxic waters since this oxygen level cannot sustain aerobic
418 metabolisms [74]. The other OMZ stations in the Pacific Ocean (PO - 102, 109, 110, 111) are
419 located in coastal areas. Although they are also under the influence of upwellings presenting
420 an oxygen depletion, the oxygen level does not achieve anoxic conditions, and thus are
421 classified as suboxic waters. This microoxic environment is enough to completely change the
422 microbial metabolism delineating the community composition in those sites. Also, differences
423 in offshore and coastal upwelling formation, for instance, or the influence of river runoffs,
424 transporting anthropogenic nutrient enrichment from the continent to coastal zones [74], could
425 be crucial to support the differences in OMZ communities we observed.

426 The same combination of OMZ anoxic and suboxic samples was observed for the pico-
427 eukaryotic groups MALV-II and Diplonemida, suggesting these OTUs as the true OMZ

428 eukaryotic signatures (Figure 4d). Some OTUs of these groups exhibited similar occurrences
429 in the anoxic Indian and Pacific Oceans but not in suboxic samples from the Pacific Ocean.
430 However, we observed a lower number of pico-eukaryotic taxa in the OMZ eco-region, the
431 prevailing OTUs being specific to Oxidic MES locations in most cases. Although the CCA
432 analysis did not disentangle the oxygen from the other variables to explain the pico-eukaryote
433 assemblage variations, here we can verify that OMZ conditions do act negatively on selection
434 of pico-eukaryotes in marine environments.

435 Another step to better understand mesopelagic community dynamics is to dissect the
436 ecological relationships among species that thrive in this layer. Co-occurrence networks can
437 indicate how the environment may structure the community acting as a filter for resident
438 species [76]. They can also give us glimpses of organisms' ecological interactions based on
439 species connectivity [76, 77]. Combining the virus, prokaryote, and pico-eukaryote data, we
440 inferred a network containing 6,154 nodes and 12,935 edges (Figure 5a, Table 3). Due to the
441 lower number of stations sampled for phages, we excluded this group from the analysis. We
442 found mainly positive relationships (94%), suggesting a predominance of putative biotic
443 interactions (e.g. competition, symbiosis) rather than taxa avoidance or exclusion. This
444 dominance of positive relations was also reported for epipelagic plankton communities [27,78].
445 The global network had a modularity value greater than 0.4 (Table 3), indicating that the
446 network has a modular structure [74]. Using a module detection algorithm, we were able to
447 identify 36 distinct modules in the global network. Three of them were mainly composed of
448 OTUs significantly enriched in mesopelagic OTUs (Oxidic MES enriched module 1 and OMZ
449 enriched modules 4 and 17; Figure 5). Together, these three modules cover almost the total
450 richness found in the mesopelagic zone (Figure 5b), and present similar values for the average
451 degree, clustering coefficient, and average path length (Table 3). These parameters indicate
452 a network complexity [76], hinting at distinct ecological niches within the mesopelagic at the
453 level of investigated organismal fractions.

454 In more detail, the OMZ signature modules were composed of a few connected nodes (323
455 and 175 nodes for modules 4 and 17, respectively), potentially indicating two distinct OMZ
456 community niches. The Oxic MES module 1 counted more nodes composing the network
457 associations (731 nodes), and both modules presented a variation in taxonomic composition
458 and proportions. OMZ module 4 contained mainly prokaryotic (23%) and girus (55%) OTUs
459 (Figure 5c, d). Among the prokaryotes, we detected taxa previously determined as OMZ
460 signatures (Nitrospinae, Marinimicrobia SAR 406, and Planctomycetes). Module 17 is mainly
461 comprised of pico-eukaryotes (82%), notably MALV-II (14%) and Diplonemida (17%)
462 previously indicated as OMZ signatures. Module 1 is taxonomically more diverse but is mainly
463 comprised of giruses and pico-eukaryotes. These groups accounted for 36% and 55%,
464 respectively, of OTUs in this module (Figure 5c, d). Giruses contributed to 598 associations
465 (edges) in mesopelagic module 1, of which 177 occurred between giruses and pico-
466 eukaryotes. Giruses from the *Mimiviridae* family are the most numerous taxa in all three
467 mesopelagic modules. *Mimiviridae* is a very abundant family in the ocean, present in various
468 size ranges from piconanoplankton (0.8-5 μm) up to mesoplankton (180- 2,000 μm) [9, 79].
469 This observation supports our findings that giruses are a prosperous group in mesopelagic
470 waters, undertaking different strategies to endure in such environmental conditions. In all three
471 modules, we observed the presence of Foraminifera, of which some species can use nitrate
472 over oxygen as an electron acceptor, favoring their survival in OMZ regions [80].

473 Sugihara [57] affirms that a hierarchical niche structure can explain the lognormal abundance
474 pattern in communities, and this assertion is valid for small assemblages and for large
475 ensembles. Consistently, the observation of three distinct community modules supports the
476 evidence of the lognormal ecological model empirically defined locally for each assemblage.
477 Our results converge and suggest that the mesopelagic presents at least three well-defined
478 ecological niches (Oxic MES, OMZ-4 and OMZ-17), with established conditions and resources
479 (abiotic and biotic) that allow the survival of a given species in these environments. Differences
480 between OMZ and Oxic MES networks suggest a potential loss of connections and interactions

481 among mesopelagic community members, directly affecting ecosystem stability due to habitat
482 change.

483

484 **Conclusions**

485

486 In this study, we explored mesopelagic pico-plankton ecological structuring, and concluded
487 that this component of oceanic plankton is heterogeneous regarding its environmental
488 parameters. The ecological parameters drive mesopelagic community assemblages, as they
489 fit niche ecological models. Although we could not identify a single driver of community
490 composition (such as temperature for sunlit ocean) for all organisms, we could pinpoint the
491 relevance of oxygen for phages and prokaryotic fractions and the relation of the former with
492 particle flux. Also, we show that water masses defined by their T/S profiles can explain the
493 differences in the observed pico-plankton structure, pointing to the role of a set of
494 environmental parameters rather than single drivers for community composition.

495 By establishing Eco-regions (Epipelagic, Oxic MES, and OMZ), we were able to discriminate
496 specific OTUs for all fractions studied. While we recovered known markers for Oxic MES and
497 OMZ regions at high taxonomic levels, we also found that most of these OTU signatures are
498 observed at low taxonomic levels, which sometimes cannot be resolved using current
499 databases. Crossing these specific OTUs with co-occurrence networks, we identified three
500 niches with biotic and abiotic conditions that characterize mesopelagic waters.

501 The limiting access to data is usually the bottleneck for knowledge about mesopelagic
502 dynamics. Our study benefits from a more significant number of organism samples and distinct
503 oceanic provinces than previous ones, allowing us to combine data to derive an expanded
504 vision of mesopelagic composition. Our results emphasize the need for better understanding
505 of mesopelagic life, in particular by improving our knowledge about oxic and oxygen-depleted
506 mesopelagic-dwelling communities, especially as climate change can be expected to expand
507 marine OMZs shortly.

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535

536

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543 **Conflict of Interest**

544

545 The authors declare that they have no conflict of interest.

546

547 **References**

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791

792 **Figure legends**

793 **Figure 1:** Geographical locations of *Tara* Oceans epipelagic and mesopelagic sampling sites
794 included in this study. Symbols: ▲ refers to epipelagic, ▼ Oxidic MES and ◆ OMZ eco-regions.
795 Symbol colors represent organism groups evaluated in the present study.

796 **Figure 2:** Ordination plot of epipelagic (left) and mesopelagic (right) communities based on
797 OTU composition based on canonical correspondence analysis (CCA). Percentages in
798 parentheses are the amount of variation constrained, in titles represent the total in each
799 analysis, and in the axis the correspondent value for each dimension. Arrows represent
800 environmental quantitative explanatory variables with arrowheads indicating their direction of
801 increase. Shapes represent sampling sites. Shape formats represent eco-regions, epi:
802 epipelagic, Oxidic MES: oxidic mesopelagic, OMZ: oxygen minimum zone mesopelagic. IO: Indian
803 Ocean, NAO: North Atlantic Ocean, NPO: North Pacific Ocean, SAO: South Atlantic Ocean,
804 SPO: South Pacific Ocean.

805 **Figure 3:** Temperature and salinity plot indicating water mass designation for all mesopelagic
806 samples. Formats represent the different oceanic basins (■ - North Atlantic Ocean, ● - South
807 Atlantic Ocean, ▲ - Pacific Ocean, ★ - Indian Ocean). Colors indicate the oxygen concentration
808 at the sampling depth. LSW - Labrador Sea Water; AAIW - Antarctic Intermediate Water;
809 tNPIW transitional North Pacific Intermediate Water; SAMW - Subantarctic Mode Water;
810 SPSTMW - South Pacific Subtropical Mode Water; modAAIW - modified Antarctic Intermediate
811 Water; PGW - Persian Gulf Water mass; RSW - Red Sea Water mass; NASTMW - North
812 Atlantic Subtropical Mode Water.

813 **Figure 4:** Relative abundance of OTUs assigned to mesopelagic eco-regions. A) Phages, B)
814 Giruses, C) Prokaryotes and D) pico-Eukaryotes.

815 **Figure 5:** Co-occurrence network in epipelagic and mesopelagic communities. A) Global
816 network, with connected modules for OMZ (purple and orange) and MES (green) highlighted.
817 B) Relative taxa abundance in each module in each station and depth. C) Relative number of
818 OTUs classified in taxonomic groups. D) Network representation of modules.

819 **Supplementary Figure 1:** Non-metric multidimensional scaling (NMDS) showing epipelagic
820 and mesopelagic community stratification for each organism group.

821 **Supplementary Figure 2:** Epipelagic and mesopelagic group dispersion based on physical-
822 chemical oceanic properties (Euclidian method). A) First two axes of PCoA. B) Dispersion of
823 distances from samples to centroids.

824 **Supplementary Figure 3:** Relative abundance of OTUs classified into different eco-regions
825 by ocean layers.

826 **Supplementary Figure 4:** Normalized relative abundance of phages and their preferred eco-
827 region.

828 **Supplementary Figure 5:** Normalized relative abundance of giruses and their preferred eco-
829 region.

830 **Supplementary Figure 6:** Normalized relative abundance of prokaryotes and their preferred
831 eco-region.

832 **Supplementary Figure 7:** Normalized relative abundance of pico-eukaryotes and their
833 preferred eco-region.

834 **Supplementary Figure 8:** Relative abundance of OTUs from taxonomic groups for epipelagic
835 and mesopelagic (Oxic MES and OMZ) samples enriched in each eco-region (UBI: ubiquitous,
836 EPI: epipelagic, Core MES: core mesopelagic, Oxic MES: oxic mesopelagic, OMZ: oxygen
837 minimum zone. A) Phages B) Giruses C) Prokaryotes D) pico-eukaryotes.

611 **Figures:**

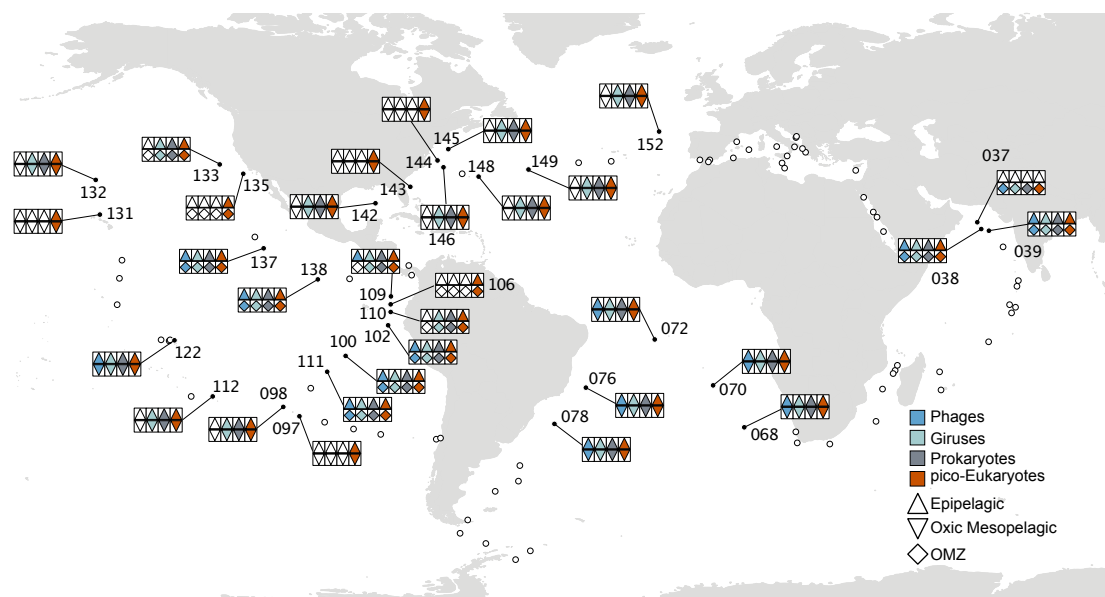


Figure 1: Geographical locations of Tara Oceans epipelagic and mesopelagic sampling sites included in this study. Symbols up-triangle refers to epipelagic, down-triangles Oxidic MES and diamond OMZ eco-regions. Symbols colors represent organism groups evaluated in the present study

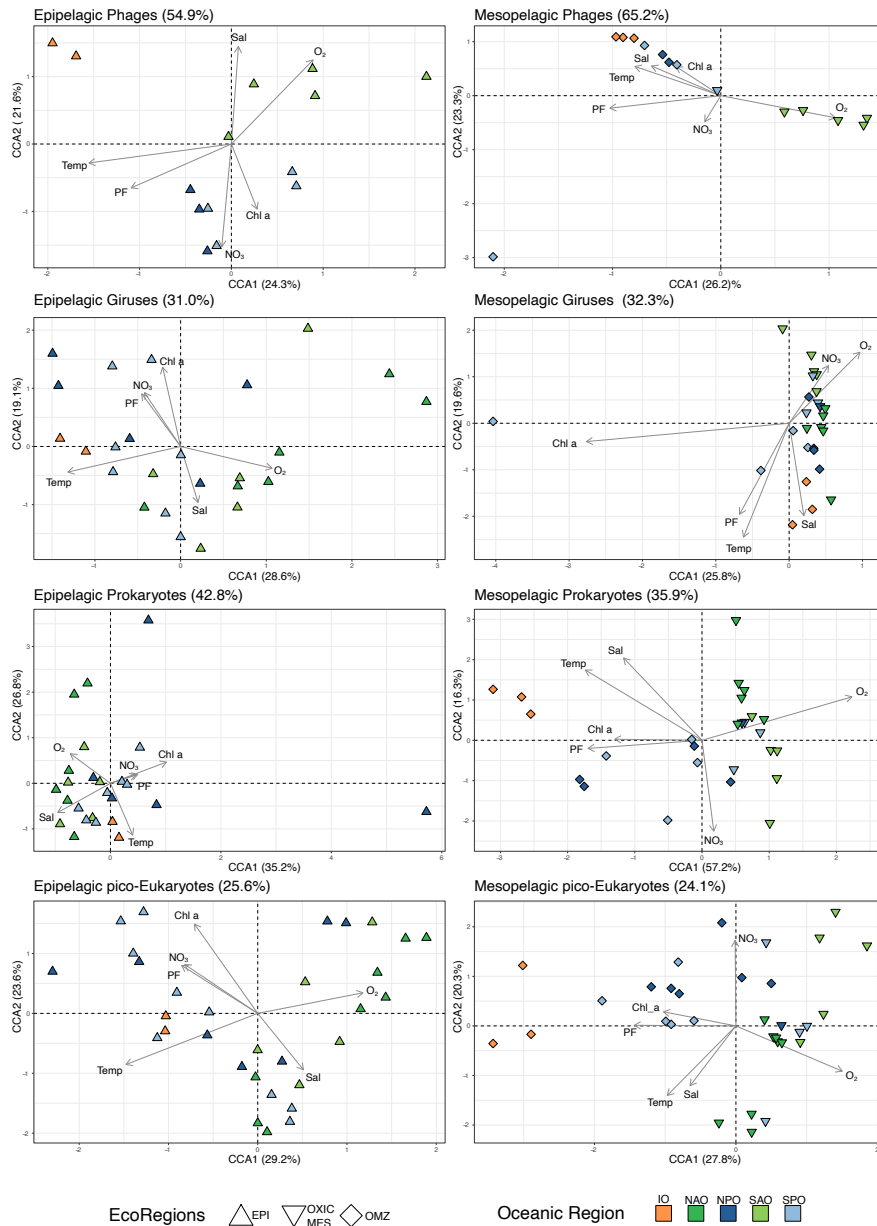


Figure 2: Ordination plot of epipelagic (left) and mesopelagic (right) communities based on OTU's composition based on canonical correspondence analysis (CCA). Percentages in parenthesis are the amount of variation constrained, in titles represents the total in each analysis, and in the axis the correspondent value for each dimension. Arrows represent environmental quantitative explanatory variables with arrowheads indicating their direction of increase. Shapes represent sampling sites. Shape formats represent eco-regions, epi: epipelagic, Oxic_mes: oxic mesopelagic, OMZ: OMZ mesopelagic. IO: Indian Ocean, NAO: North Atlantic Ocean, NPO: North Pacific Ocean, SAO: South Atlantic Ocean, SPO: South Pacific Ocean

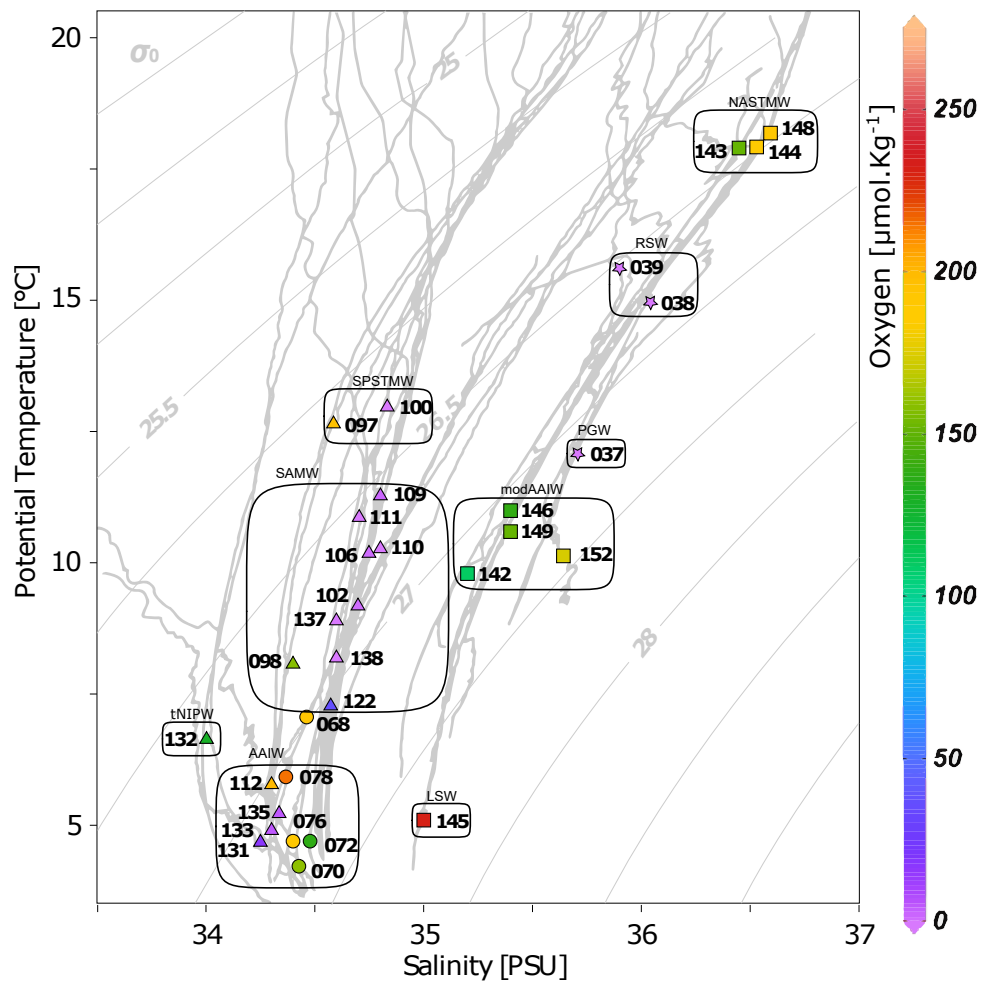


Figure 3: Temperature and salinity plot indicating water masses designation for all mesopelagic samples. Formats represent the different oceanic basins (\square - North Atlantic Ocean, \circ - South Atlantic Ocean, \triangle - Pacific Ocean, \star - Indian Ocean). Colours indicate the oxygen concentration at the sampling depth. LSW - Labrador Sea Water; AAIW - Antarctic Intermediate Water; tNIPW ? transitional North Pacific Intermediate Water; SAMW - Subantarctic Mode Water; SPSTMW - South Pacific Subtropical Mode Water; modAAIW - modified Antarctic Intermediate Water; PGW - Persian Gulf Water mass; RSW - Red Sea Water mass; NASTMW - North Atlantic Subtropical Mode Water.

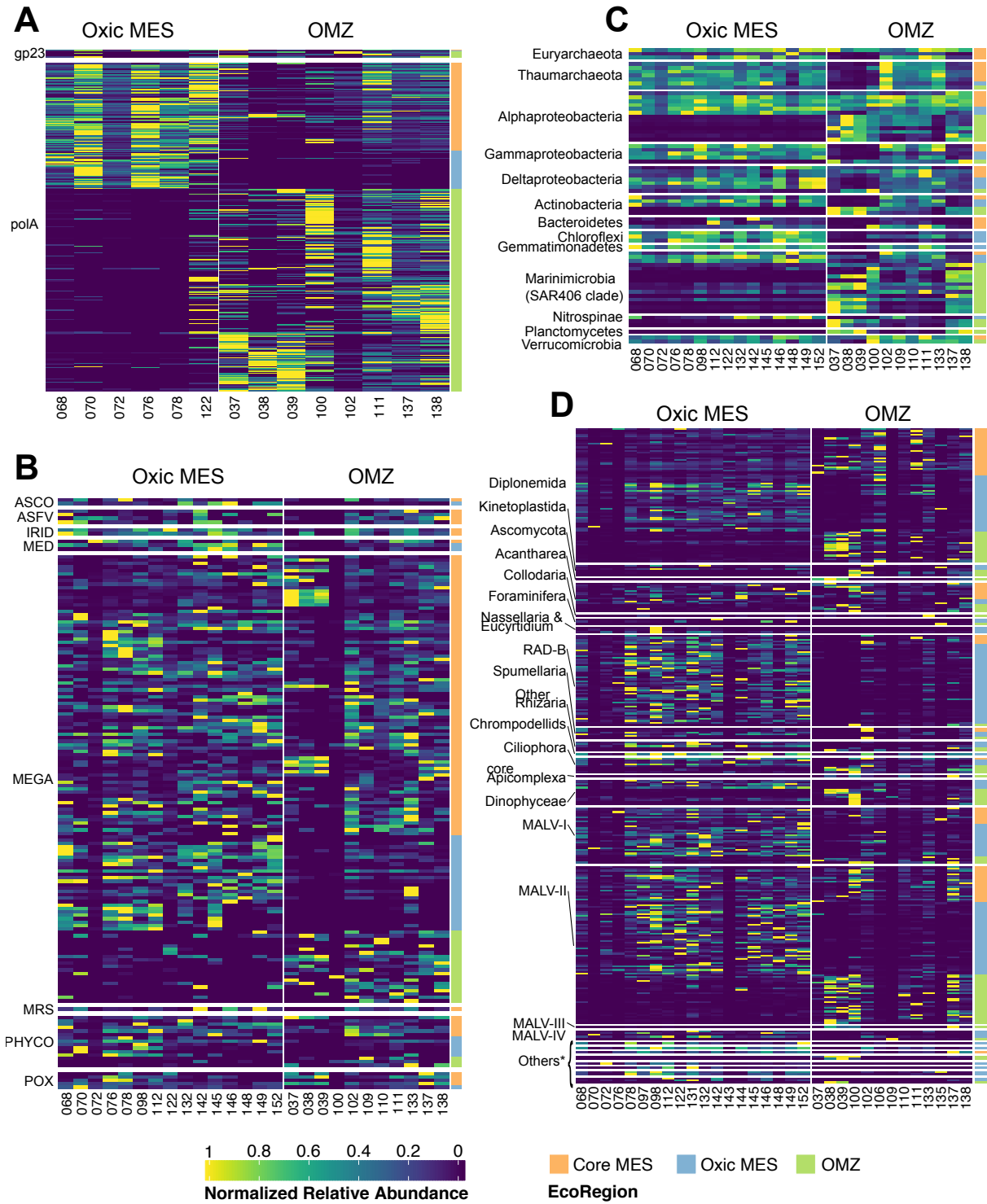


Figure 4: Relative abundance of OTUs assigned to Mesopelagic Eco-regions. A) Phages, B) Giruses, C) Prokaryotes and D) Eukaryotes

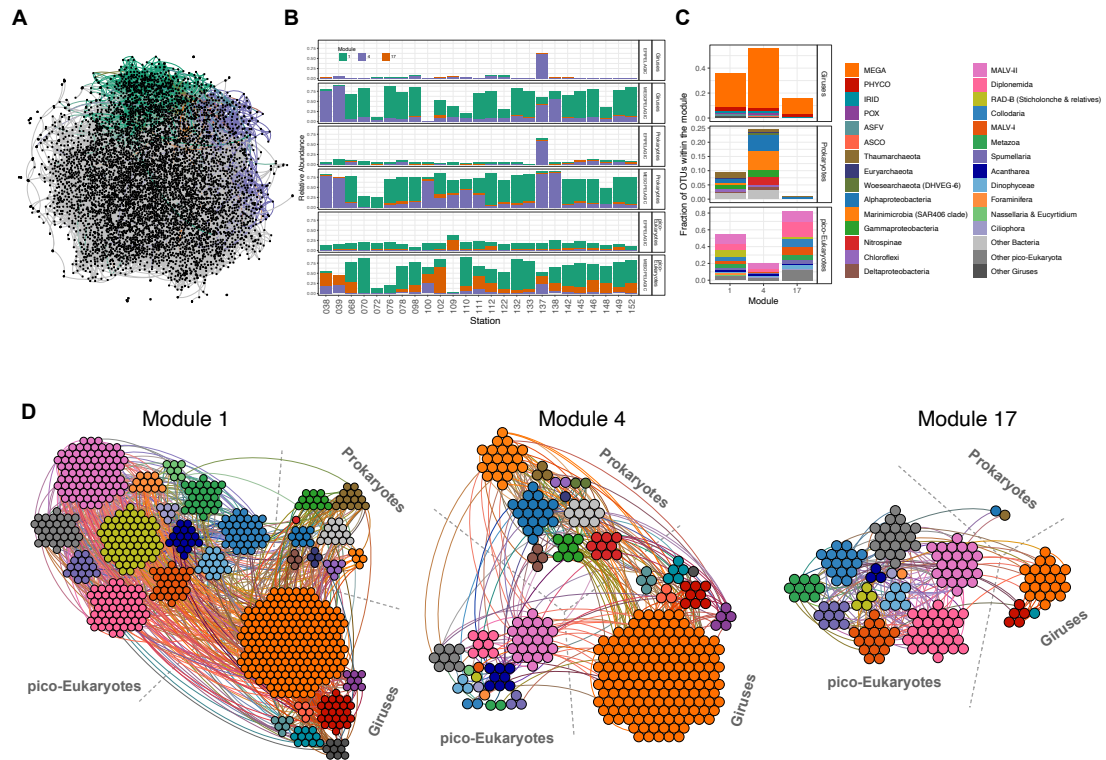


Figure 5: Co-Occurrence Network in Epipelagic and Mesopelagic communities. A) Total Network, with connected modules for OMZ (purple and orange) and MES (green) highlighted. B) Relative taxa abundance in each Module in each station and depth. C) Relative number of OTUs classified in taxonomic groups. D) Network representation of modules

612 **Tables**

Table 1: ANOVA p-value for each environmental factor used as explanatory variable. Global correspond to the p-value for the whole set of variables, the following columns to p-values for each of the environmental variables considering the others as covariable.

assemblage	Depth	Global	Temp. °C	Salinity	O ₂ [μ mol/kg]	[NO ₃] ⁻ [μ mol/l]	Chl-a [μ g/m ³]	Particle flux
Phages	EPI	0.001	0.057	0.144	0.043	0.031	0.420	0.017
Phages	MES	0.001	0.059	0.004	0.027	0.124	0.110	0.002
Giruses	EPI	0.001	0.023	0.074	0.051	0.152	0.053	0.221
Giruses	MES	0.002	0.032	0.211	0.145	0.134	0.008	0.211
Prokaryotes	EPI	0.035	0.048	0.141	0.002	0.006	0.044	0.568
Prokaryotes	MES	0.006	0.501	0.304	0.039	0.444	0.966	0.486
pico-Eukaryotes	EPI	0.025	0.027	0.166	0.412	0.292	0.216	0.659
pico-Eukaryotes	MES	0.001	0.606	0.191	0.243	0.468	0.271	0.477

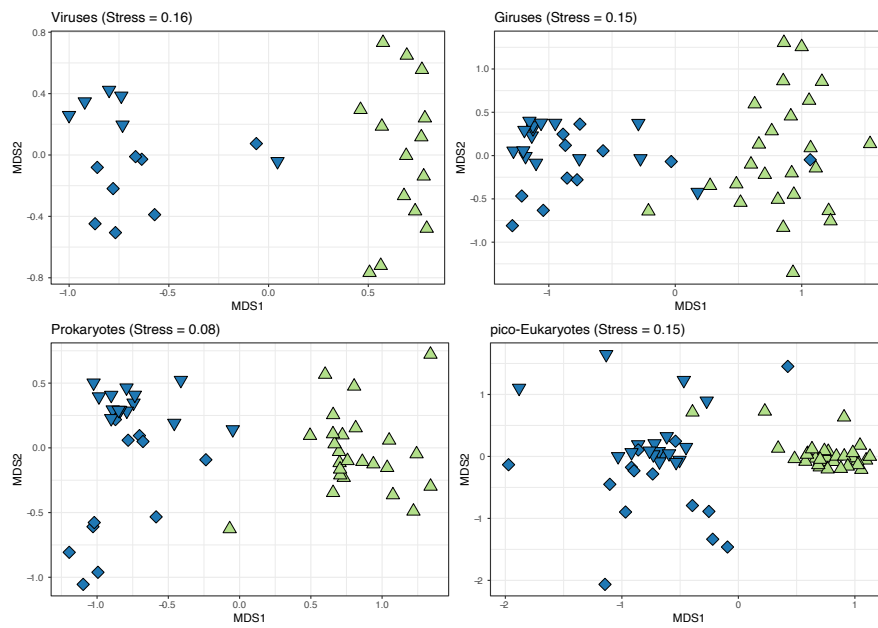
Table 2: Proportion of the variation in community composition that explained by water masses using the Permutation multivariated analysis of variance (PERMANOVA)

assemblage	Df	Sum Of Squares	Mean Squares	F. Model	R ²	Pr(χ^2 F)
Phages	4	1.87	0.47	2.32	0.51	0.002
Giruses	8	3.19	0.40	1.81	0.46	0.001
Prokaryotes	8	1.30	0.16	3.29	0.60	0.001
pico-Eukaryotes	8	2.60	0.32	1.62	0.36	0.001

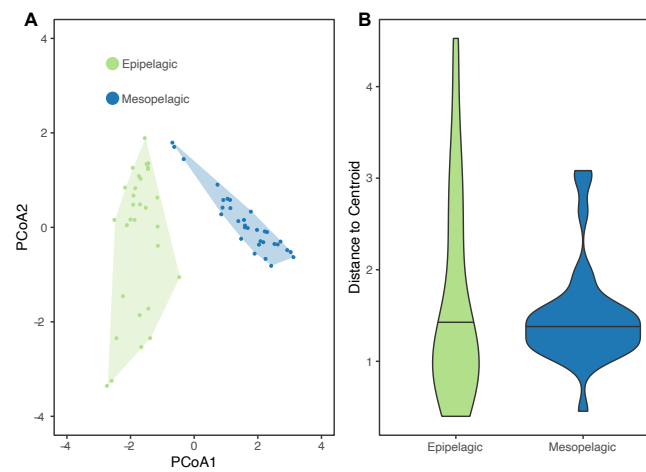
Table 3: Network topological features derived from global analysis including giruses, prokaryotes and pico-eukaryotes samples in epipelagic and mesopelagic depths

Name	Global	Mod 1	Mod 4	Mod 17
Nodes	6154	731	323	175
Positive Edges	12193	1236	480	223
Negative Edges	742	70	49	9
Avg. degree	4.20	3.57	3.28	2.65
Clustering	0.03	0.03	0.09	0.05
Density	0.00	0.00	0.01	0.02
Average.path.length	7.28	6.01	6.27	6.30
Betweenness	0.01	0.05	0.10	0.22
Degree Centralization	0.00	0.01	0.02	0.04
Modularity	0.47	0.60	0.67	0.66

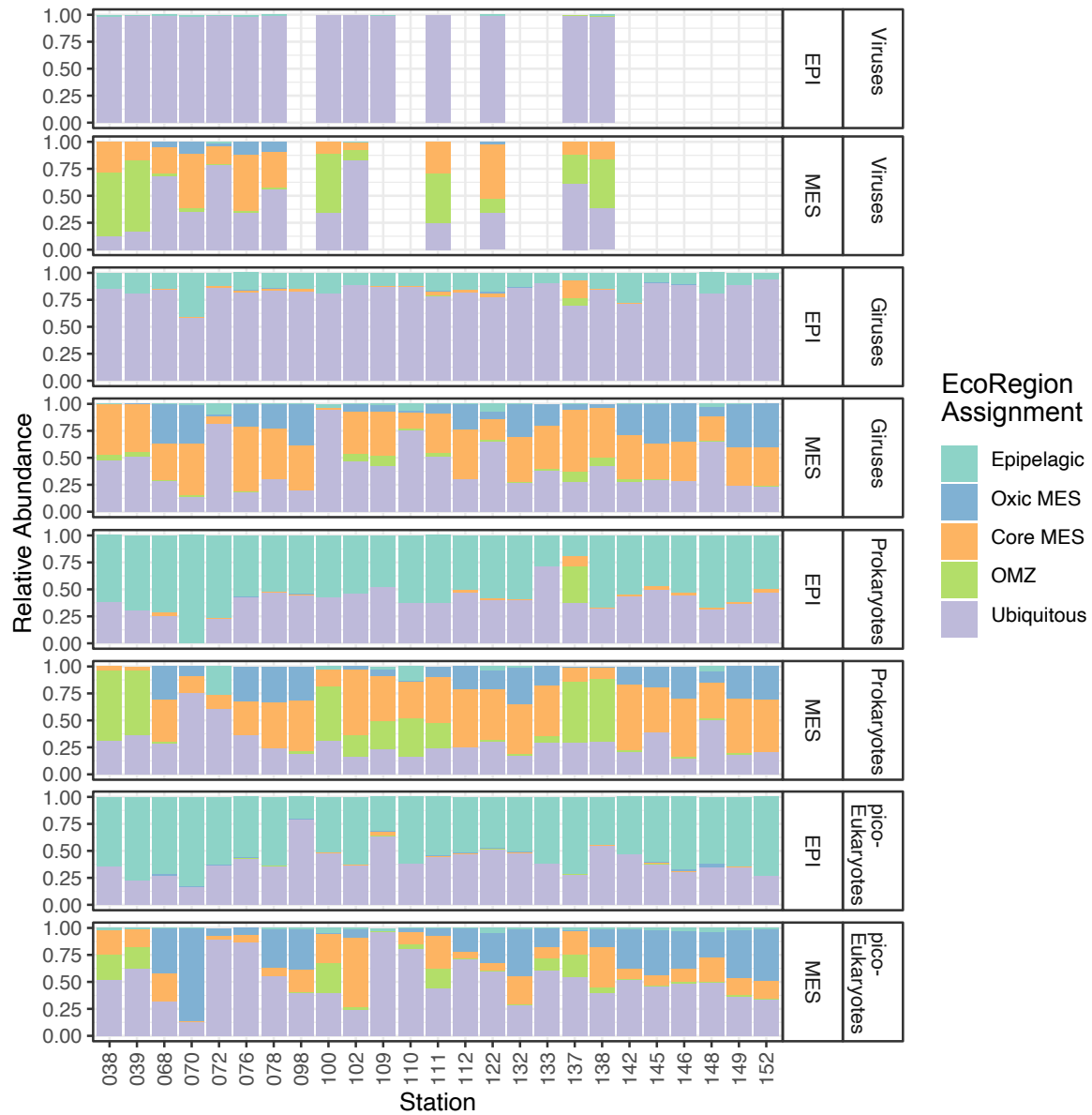
613 **Supplementary Figures:**



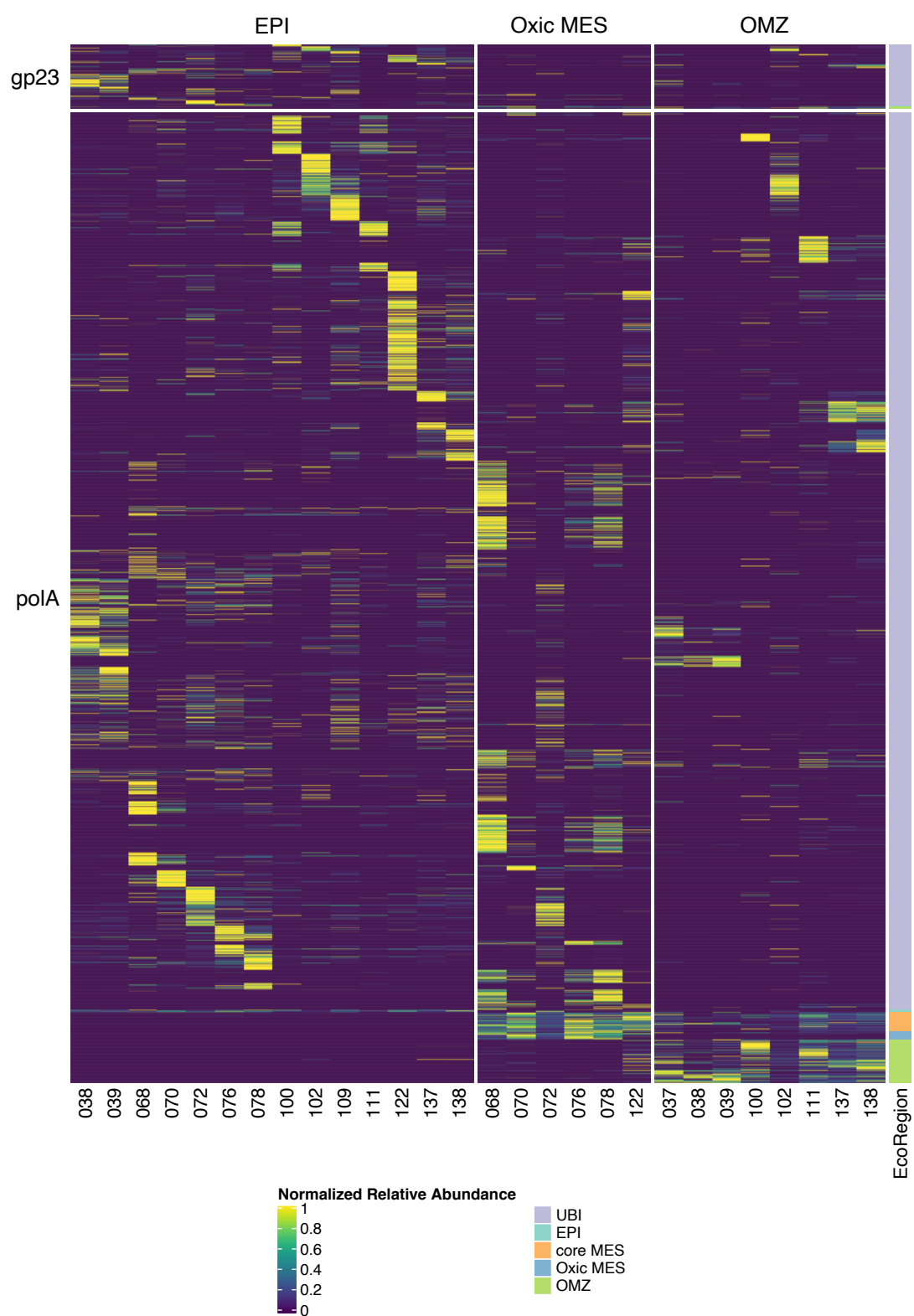
Supplementary Figure 1: Non-metric multidimensional scaling (NMDS) showing epipelagic and mesopelagic communities stratification for each organism group



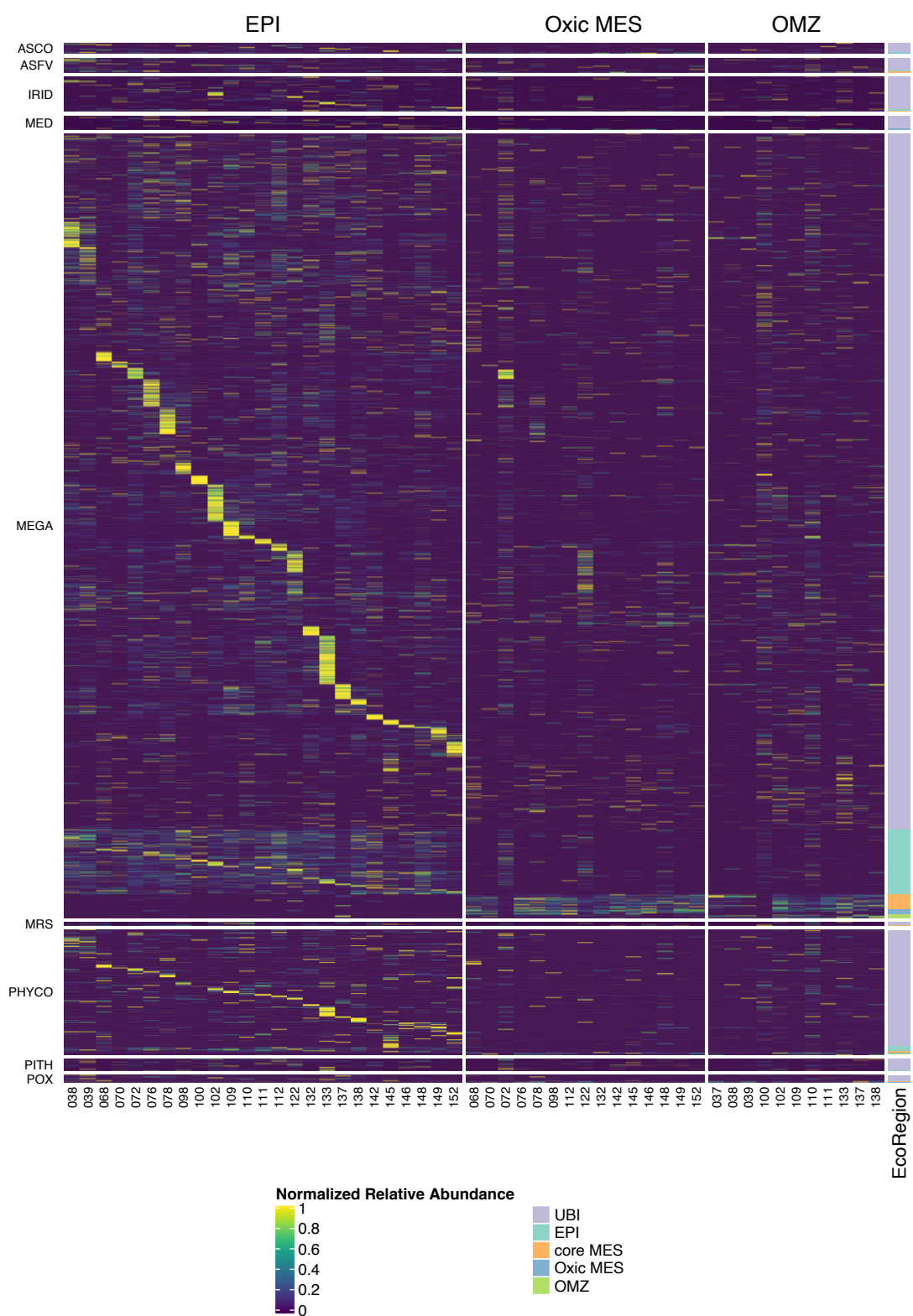
Supplementary Figure 2: Epipelagic and mesopelagic group dispersion based on physical-chemical oceanic properties (Euclidian method). A) First two axes of PCoA. B) Dispersion of distances from samples to centroids.



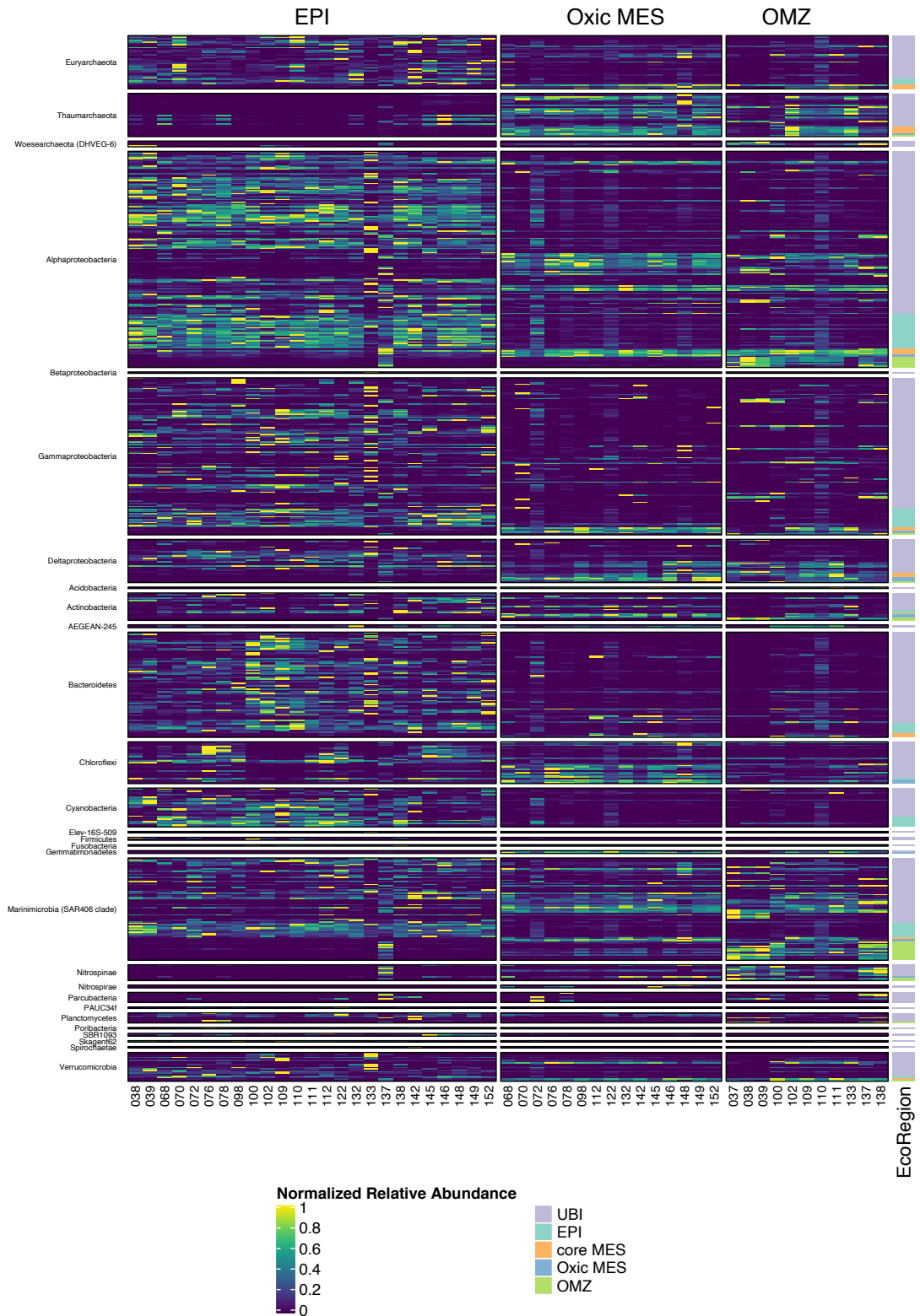
Supplementary Figure 3: Relative abundance of OTUs classified into different eco-regions in to ocean layers



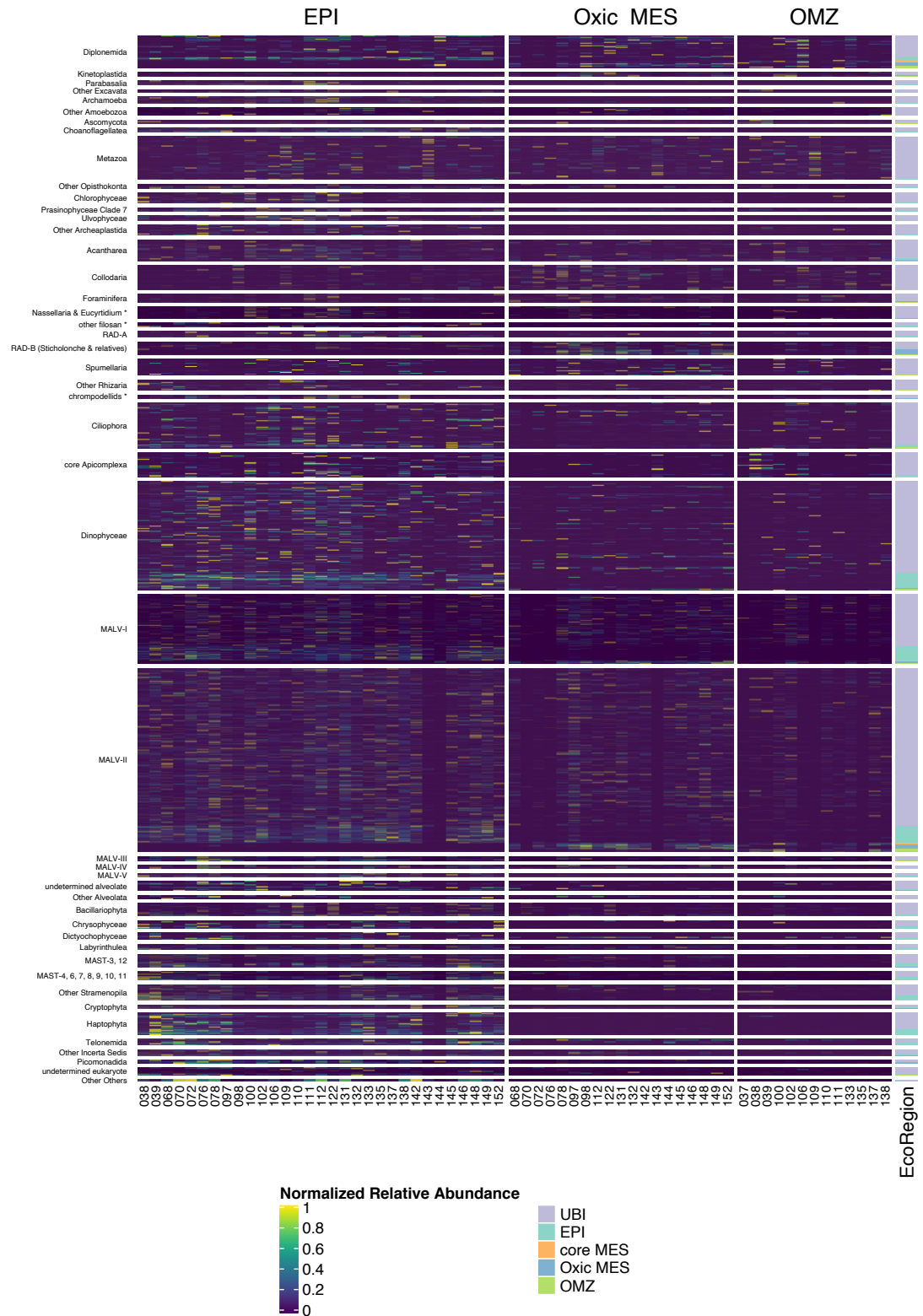
Supplementary Figure 4: Normalized Relative abundance of Phages and their preferred eco-region



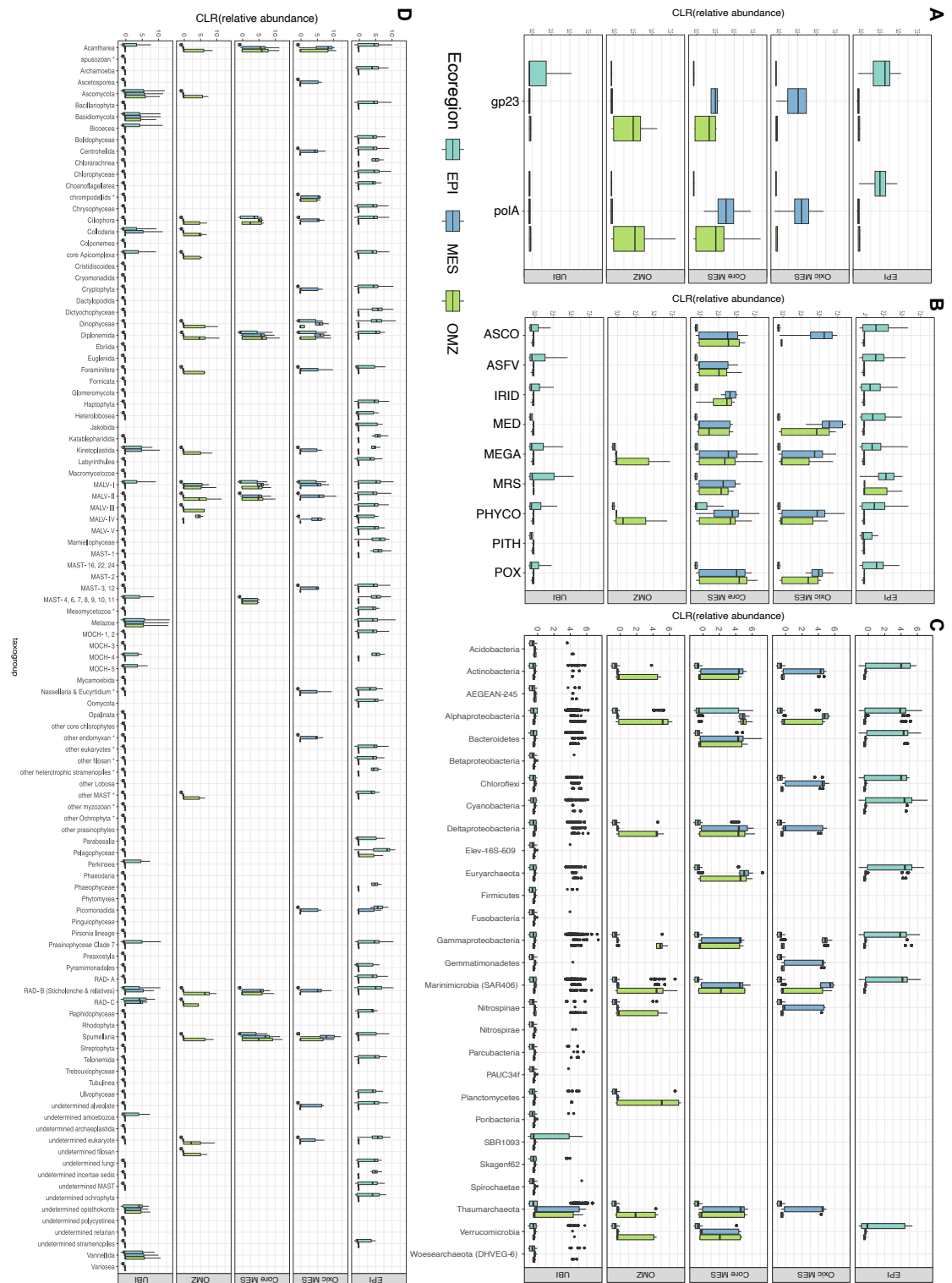
Supplementary Figure 5: Normalized Relative abundance of giruses and their preferred eco-region



Supplementary Figure 6: Normalized Relative abundance of Prokaryotes and their preferred eco-region



Supplementary Figure 7: Normalized Relative abundance of pico-Eukaryotes and their preferred eco-region



Supplementary Figure 8: Relative abundances of OTUs from taxonomic groups for epipelagic and mesopelagic (Oxic MES and OMZ) samples enriched in each eco-region (UBI: ubiquitous, EPI: epipelagic, Core MES: core mesopelagic, Oxic MES: oxic mesopelagic, OMZ: oxygen minimum zone). A) Phages B) Giruses C) Prokaryotes D) pico-Eukaryotes