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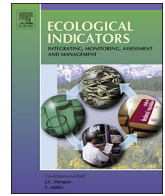
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# Coastal eutrophication as a potential driver of functional homogenization of copepod species assemblages in the Mediterranean Sea

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## ABSTRACT

Eutrophication as a consequence of anthropogenic nutrient enrichment is one of the major threats to biodiversity in nearshore and coastal marine waters, and consequently, for ecosystem functioning. This study explores changes in the biological organization of copepod assemblages along a Chl *a* gradient through an upscaling analysis of regional datasets from the coastal waters of the Mediterranean Sea. Results show that omnivorous copepods using passive and/or ambush feeding strategy are favored as Chl *a* increases, and copepod community shifts towards trophic homogenization by favoring generalist feeders against specialists. To our knowledge, this is the first report of functional homogenization of copepods as the result of eutrophication. The present study also demonstrates the potential use of trait-based approaches to explore the effect of human disturbances on marine copepod assemblages in marine ecosystems.

## 1. Introduction

Coastal eutrophication as a result of anthropogenic nutrient enrichment is one of the major threats to biodiversity (Halpern et al., 2008; Howarth, 2008; Vitousek et al., 1997), and therefore, for the stability of ecosystems and the functions and services they provide (Cardinale et al., 2012; Hautier et al., 2015; Hooper et al., 2012; Zhang et al., 2016). Besides the increase in primary production, nutrient enrichment may induce profound compositional, functional, and/or genetic changes of species assemblages (e.g. Alexander et al., 2017; Cloern, 2001; Nelson et al., 2013). In particular, nutrient enrichment may impoverish ecological communities by selecting more closely related species and/or replacing progressively specialists by generalists resulting from the narrower niche breadth of the first ones and their lower tolerance to high nutrient levels. Because specialists are considered to be efficient at capturing and consuming resources, it is expected that their loss may affect greatly the transfer of energy within the ecosystem (Alexander et al., 2017; Olden et al., 2004). Such eutrophication-driven biotic homogenization, which may occur without species loss and/or change in taxonomical diversity (Larsen et al., 2018), has been highlighted in: a) terrestrial plants (Buhk et al., 2017; Bühler and Roth, 2011); b) various kinds of freshwater organisms (fish: Menezes et al., 2015; Villéger et al., 2014; diatoms: Wengrat et al.,

2018; daphniids: Rogalski et al., 2017; and benthic invertebrates: Donohue et al., 2009; Zhang et al., 2019); and c) marine fish (Alexander et al., 2017). Several studies have shown that while specialists and generalists have the same probability of extinction, specialists encounter difficulty in recolonizing a site (Larsen et al., 2018, and reference therein). Hence, given the potential complexity of the responses of species assemblages to eutrophication, appropriate metrics and a systematic examination of different facets of biodiversity are needed to better understand the effect of eutrophication on biodiversity. And in so doing, this will guide efforts to better manage, preserve, and ensure the sustainable use of coastal ecosystems.

Taxonomical-based diversity indices are widely used under the context of the EU Water Directive and the Marine Strategy Framework Directive (EU MSFD) to assess the ecological and environmental status of marine waters (Birk et al., 2012). However, since taxonomical-based metrics do not consider functional traits of organisms (e.g. feeding behavior, environmental tolerance, vulnerability to predation, etc.), they often fail to detect the effect of human pressures on biodiversity (Dornelas et al., 2014; Hillebrand et al., 2017; Lindenmayer et al., 2015; Villéger et al., 2010). For the same reasons, taxonomical-based diversity indices cannot detect some major driving mechanisms of community assembly, such as environmental filtering and biotic interactions (Cornwell and Ackerly, 2009). In contrast to traditional

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taxonomic metrics, functional ones relate to niche processes based on the use of functional traits are better descriptors of the effect of anthropogenic stress on species assemblages, and have the potential to act as an early warning signal for the deterioration of an ecosystems (Cadotte et al., 2011; Mouillot et al., 2013; Villéger et al., 2010). In other words, trait-based approaches may help to elucidate ecological processes, as well as, the underlying mechanisms structuring communities and driving critical ecosystem functions. Furthermore, there is the possibility to compare different systems composed of distinct species assemblages and make predictions (McGill et al., 2006).

The open Mediterranean Sea is characterized by high diversity and oligo- ultra-oligotrophic waters (Coll et al., 2010). However, many coastal Mediterranean areas suffer from eutrophication (Micheli et al., 2013). Most of the monitoring studies consider phytoplankton since it is directly affected by nutrients (e.g. Brucet et al., 2013). Yet, exploration of the functional response of the copepod community could also inform us on the quality of the ecosystem. Copepods dominate zooplankton communities; they play a pivotal role in the link between primary production and higher trophic levels (e.g. Beaugrand et al., 2003) in the recycling of nutrients and dissolved organic matter (Mitra et al., 2014); and their community structure is sensitive to environmental pollution (e.g. Siokou-Frangou and Papathanassiou, 1991; Uriarte and Villate, 2005; Uye, 1994). Accordingly, a directional change in functional dominance, i.e. towards smaller-sized and pollution tolerant/opportunistic copepod species, have been reported in some regions - although not rigorously quantified (e.g. Intxausti et al., 2012; Siokou-Frangou and Papathanassiou, 1991; Uye and Sano, 1998). The present study aimed to fill this gap by examining through an upscaling of original and existing data in the Mediterranean Sea functional trait, functional diversity, and functional specialization of copepod communities across a Chl *a* gradient as a proxy of eutrophication. Their consistency relative to an expected deterioration of the ecosystem as a consequence of eutrophication was also considered. For that trait data of total body length, trophic regime, feeding mode and feeding strategy were used (Benedetti et al., 2016).

## 2. Material & methods

### 2.1. Datasets

Twelve studies of copepod abundance data were selected based on the following criteria: (i) all the samples were collected in the upper 50 m together with Chlorophyll *a* (Chl *a*) data, which was collected at the same time as the copepods, or obtained from satellite databases, (ii) abundance data referred to adult copepods and copepodites (Fig. 1, Table 1) except at Gulf of Gabes (see below) where nauplii were considered too because the authors of the existing datasets aggregated them with the other copepod stages. Given the low contribution of nauplii to this site (a maximum of 5% of the total copepod abundance) and the total data points (3 points over a total of 162) used for GLMM analysis (see 2.4. Model description) it was considered that they had insignificant influence on the overall outcome of the analysis. (Fig. 1, Table 1). These 12 field studies included the coastal waters of the: Alboran Sea (Berraho et al., 2016); Thyrrenian and Adriatic seas (Busatto, 2007; Mazzocchi, 2008a,b,c; Ragosta et al., 1995); Ligurian Sea (Dauby, 1980); Northeastern Aegean Sea (Siokou-Frangou and Papathanassiou, 1991; Isari et al., 2006), the Gulf of Annaba (Khelifi-Thouami et al., 2007), the Gulf of Gabes (Drira et al., 2017); Bay of Tunis (Ben Lamine et al. 2015); Nile delta (Eltohamy et al., 2017); and Iskenderun Bay (Kurt and Polat, 2013) in the eastern basin. Added to these datasets was an original field study realized in the Bay of Jijel within the Algerian basin (Western Mediterranean Sea) at three stations (S1: 36.83°N, 5.85°E; S2: 36.83°N, 5.79°E, and S3: 36.78°N, 5.57°E, cf. Fig. S1) over an annual cycle in the first 30 m of depth (2016–2017, 33 samples). The net mesh size used in all these studies ranged from 54 to 300  $\mu\text{m}$  (Table 1). The 300  $\mu\text{m}$  mesh used at the Bay of Jijel could

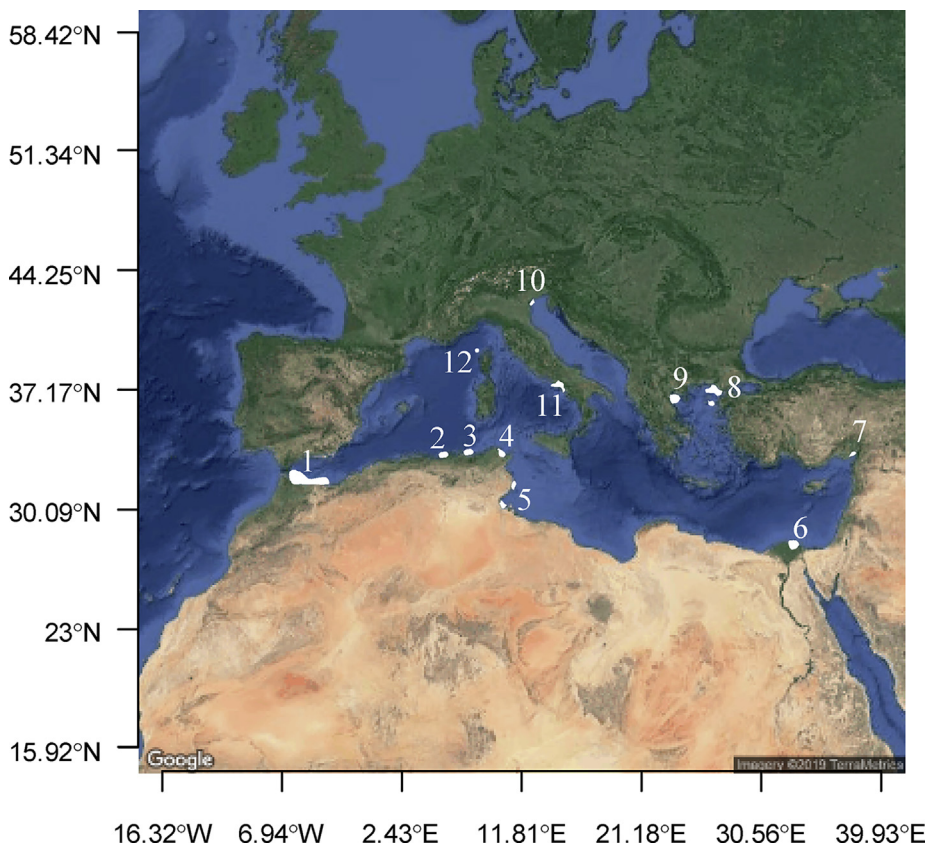
potentially underestimate the abundance of the smallest copepod species ( $\leq 300 \mu\text{m}$ ) such as the genera *Oncaea* (species *minima*, *vodjanitskii*, *atlantica*, *longipes*, *mollicula*, *tenella*, and *tregoubovi*) and *Spinoncaea* (species *humesi* and *tenuis*) (Brun et al., 2017; Hirst and Kjørboe, 2014; Razouls et al., 2005–2019). However, given that these species occur mainly in the Adriatic and Ionian Seas and in the eastern Mediterranean Sea (Razouls et al., 2005–2019), and that they were absent from the two adjacent studied areas (Morocco and Annaba coastal waters), where a smaller net mesh size (147 and 200  $\mu\text{m}$ ) was used (Table 1), it was assumed that there had been no underestimation of the smallest species in this dataset. Each study included multiple stations, and/or several seasonal campaigns, representing altogether, a total of 162 samples at a monthly scale and with environmental data (Table 1). They included 4 orders, 73 genera, and 217 species, over a total richness of 561 copepod species recorded in the Mediterranean Sea and the Black Sea (Razouls et al., 2005–2019); after taxonomy updating using the World Register of Marine Species (WoRMS, <http://www.marinespecies.org/aphia.php?p=webserve>). The final copepod species abundance datasets are given in Table A1. In addition, salinity, Chl *a* and seawater temperature data (Table A2) associated to the copepod datasets were used. Missing Chl *a* data for copepod sampling from 2002 (i.e. Bay of Jijel, NE Aegean Sea, Northern Adriatic Sea, and Annaba CW) were extracted from the MODIS-Aqua ocean color sensor available at [https://oceanwatch.pifsc.noaa.gov/erddap/griddap/OceanWatch\\_aqua\\_Chla\\_monthly.html](https://oceanwatch.pifsc.noaa.gov/erddap/griddap/OceanWatch_aqua_Chla_monthly.html). In addition, the mean of the temperature values of the closest stations were used for the lacking temperature data in the Bay of Thessaloniki and the Gulf of Theirmaikos, and salinity data from Goffart et al. (2002) were used for the Bay of Calvi.

### 2.2. Copepod traits

Most of the trait data were obtained from the recent Mediterranean copepod trait database provided by Benedetti et al. (2016) and completed by those of Hirst and Kjørboe (2014), and Brun et al. (2017). Traits with the most complete coverage of the copepod species included in the present study were chosen, i.e. total body length (mm), trophic regime (herbivore, carnivore, detritivore), feeding mode (passive, active, and mixed feeding), and feeding strategy (filter, cruise, and active ambush feeding) (Table 2). All of these traits influence fitness indirectly through growth, reproduction, and/or survival (Kjørboe and Hirst, 2014; Litchman et al., 2013), and most of them have been shown to be responsive to environmental condition change including Chl *a* concentrations (McGinty et al., 2018). For each species, the degree of herbivory (or carnivory) was calculated by applying a coefficient of 1/3 (or 1/3) for omnivore, 2/3 (or 1/8) for omnivore-herbivore, and 1/8 (or 1/8) for omnivore-detritivore species, 0 (or 1) for carnivore, and 1/8 (2/3) for omnivore-carnivore (Table 2). As a result, for 25% of the species present in this study, no trait information was found. When missing, trait values of copepod species were completed using information available at the genus level or higher. When copepodites were identified at the genus (NE Aegean Sea and Iskenderun Bay) or order level (Egypt coastal waters), the trait values were assessed by considering only the adult copepod species recorded at this site and belonging to the same taxonomical level. The final compiled trait values used in this study are given in Table A3 (see supplementary data). These include 166 copepod species with a complete coverage of trait values, and 52 species (26 calanoid, 16 cyclopoid, 8 harpacticoid, and 2 Monstrilloid species) with incomplete coverage in trophic trait values.

### 2.3. Functional diversity metrics and functional homogenization

Functional identity (also called functional dominance) was estimated as the community-weighted mean of trait values (CWM; Garnier et al., 2004). Concerning functional diversity indices, functional dispersion (FDis), according to Laliberté and Legendre (2010), was calculated. For this, only the traits responding to the environment (and



**Fig. 1.** Location of the Mediterranean sampling areas used in this study. (1) Morocco coastal waters, (2) Bay of Jijel (Algeria), (3) Annaba coastal waters (Algeria), (4) Gulf of Tunis (Tunisia), (5) Gulf of Gabes (Tunisia), (6) Nile estuary/Diametta harbour/Coastal waters (Egypt), (7) Bay of Iskenderun (Turkey), (8) NE Aegean Sea (Greece), (9) Bay of Thessaloniki/Gulf of Theirmaikos (Greece), (10) Northern Adriatic Sea (Italy), (11) Tyrrhenian coastal waters (Italy), and (12) Bay of Calvi (Corsica, France). Each one included several sampled stations and/or sampling dates for a total of 162 samples with environmental data available (see Table I for details). The map was built with the 'ggmap' package (Kahle and Wickham, 2013).

consequently being functional) were used, i.e. those for which a significant relationship between CWMs and Chl *a*, seawater temperature, and/or salinity was found. All the functional community components were calculated using the 'FD' package (Laliberté and Legendre, 2010), after the log-transformation of species abundances at the different sampling stations/sites, to reduce the effect of potential outliers. The CWM corresponds to the mean trait value amongst each community, weighted by the relative abundance of each species (Garnier et al., 2004). To reduce the number of copepod species for which trait data were not available (maximum of 14% at Damietta harbor in Egypt), CWMs were calculated per datasets and per trait. By applying such procedure, the percentage of copepod species abundance with no trait information was always < 10% except for Egypt (14 and 10% for Damietta harbor and Estuary downstream, respectively). This 14% maximum was lower than the threshold limit of 20% of the total copepod abundance for CWMs to being representatives of the entire copepod species community (Pakeman and Queded, 2007). FDis is the mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre, 2010). One of the advantages of FDis is that it is unaffected by species richness by construction (Laliberté and Legendre, 2010). In such cases, there is no need to estimate from the deviation (standardized effect size [SES]; Gotelli and McCabe, 2002) of the observed functional diversity of one copepod community from that expected from a random community (e.g. Breton et al., 2017). FDis were calculated for each pair of functional traits and for all combined functional traits. To calculate the multidimensional trait space, a preliminary principal coordinate analysis (PCoA) was performed, with the traits on a matrix of Gower distances (Podani, 1999), which account for the different types of traits (numeric, binary, and ordinal). All the axes of the PCoA were retained. Then, the Podani method and Lingoes correction (Lingoes, 1971) was applied to obtain Euclidean distance matrices. The precision of functional diversity indices is more sensitive to the incompleteness in species trait data than CWMs (Pakeman, 2014). However, this same author showed also that

FDis was the functional diversity indicator the least affected by the incompleteness in trait data, with a deviance at a maximum of 3.5% (Pakeman, 2014). Finally, functional homogenization was calculated according to Mondy and Usseglio-Polatera (2014). Given the incomplete information on the minimum and maximum value of the trait's total body length, only the trophic traits (trophic regime, feeding mode, and feeding strategy) were used for the calculation of functional homogenization. For each copepod species and each trophic trait, a Taxon Specialization Index (TSI) was first calculated using the Gini-Simpson index formula (Gini, 1912; Simpson, 1949). Then, each TSI was scaled by its respective minimum and maximum values to account for the different number of categories among traits (Mondy and Usseglio-Polatera, 2014). Finally, trophic homogenization as Community Specialization Index, which varies from 0 (truly generalist) to 1 (truly specialist), was calculated as the CWMs of each TSI.

#### 2.4. Model description

To evaluate how the whole community composition of copepods differed between stations/sites and seasons, a non-metric multidimensional scaling (nonparametric method nMDS, Taguchi and Oono, 2005) based on Bray-Curtis dissimilarity was performed using the matrix of species abundances with the 'Vegan' package (Oksanen et al., 2011). Prior to this, the abundance matrix was subject to square-root transformation, followed by a Wisconsin double standardization. Significance of nMDS was tested using Permutova (function *Adonis* in 'Vegan' package) with 10,000 permutations of the raw data, and goodness of fit was evaluated based on stress *S* ( $S < 0.05$  as excellent representation in reduced dimensions, < 0.1 great, < 0.2 good, and stress > 0.3 poor). Relationships between environmental variables and the MDS axes were investigated with *bioenv()* function (Clarke and Ainsworth, 1993; Oksanen, et al., 2011). To explore the difference between sites, a post-hoc pairwise comparison test was performed using the pairwise.adonis 'pairwise.adonis' function (Martinez Arbizu, 2019).

**Table 1**  
Description of the Mediterranean datasets used in this study (between brackets: number of sampled stations).

Map code	Location	Coordinates	Period	Sampling frequency	N samples*	Net mesh size (µm)	Reference
1	Morocco coastal waters	35.1–35.9°N; 2.2–5.5°W	2013	1 spring campaign (61)	1	147	Berraho et al., 2016
2	Bay of Jijel (Algeria)	36.78–36.83°N; 5.57–5.85°E	2016–2017	Monthly (3)	33	300	This study
3	Gulf of Annaba (Algeria)	36.9–37°N; 7.9–8°E	2002–2003	5 seasonal campaigns (3)	5	200	Khelifi-Thouami et al., 2007
4	Gulf of Tunis (Tunisia)	36.7–37.17°N; 10.18–11.08°E	2007–2008	5 seasonal campaigns (5)	25	220	Ben Lamine et al., 2015
5	Gulf of Gabes (Tunisia)	33–35°N; 10.7–10.8°E	2014	October/November (30)	3	100	Drira et al., 2017
6	Nile estuary/Diametta harbour/Coastal waters (Egypt)	31.47–31.53°N; 31.77–31.85°E	2014	June/July (16)	3	54	Eltohamy et al., 2017
7	Bay of Iskenderun (Turkey)	36.82–36.84°N; 35.82–35.91°E	2008	4 seasonal campaigns (5)	4	200	Kurt and Polat, 2013
8	NE Aegean sea (Greece)	39–41°N; 24.5–26°E	2003	2 summer campaigns (32)	2	200	Isari et al., 2006
9	Bay of Thessaloniki/Gulf of Thermaikos (Greece)	40.37–40.62°N; 22.68–22.9°E	1984–1985	3 seasonal campaigns (10)	28	200	Stokou-Frangou and Papatheanassiou, 1991
10	N Adriatic (Tegnie & Chioggia coastal waters, Italia)	45.2–45.32°N; 12.38–12.72°E	2006–2007	4 seasonal campaigns (4)	15	200	Busatto, 2007
11	Thyrrrenian coastal waters	40.25–40.84°N; 13.66–14.88°E	1986–1987	3 seasonal campaigns (23)	37	200	Ragosta et al., 1995; Mazzocchi, 2008a,b,c
12	Bay of Calvi (Corsica, France)	42.58°N; 8.72°E	1978–1979	Daily (1)	7	180	Dauby, 1980

\*Number of samples available and for which data of seawater temperature and salinity and chlorophyll *a* are available.**Table 2**

Copepod traits used in this study. Most of the trait values have been gathered in copepod databases (Benedetti et al., 2016; Brun et al., 2017; Hirst and Kiørboe, 2014).

Trait	Type	Range/Category	Sub-category
Total body length	Continuous	0.39–8.5 mm	
Trophic regime	Fuzzy coded 0.2,0.5,0.75,1	Carnivory (C)	C = 1 <sup>a</sup>
		Herbivory (H)	Omnivory-C = 0.75 <sup>a</sup>
		Detritivory (D)	Omnivory = 0.5 <sup>a</sup> Omnivory-H = 0.2 <sup>a</sup> Omnivory-D = 0.2 <sup>a</sup>
Feeding mode	Ordinal	Passive = 0 Mixed = 0.5 Active = 1	
Feeding strategy	Fuzzy coded 1,0	Filter Cruise Ambush Particle Parasite	

a: values assigned for trait carnivory given as example.

In order to account the potential non-independence of station and seasonal samples within sites (random effect), the effect of Chl *a*, seawater temperature and salinity on copepod community composition, and different facets of copepod biodiversity, were evaluated using Generalized Linear Mixed Models (GLMM, Zuur et al., 2009). After identification of potential outliers in the response variables via box plot analysis, each GLMM model was sequentially built with backward model selection, and with the predictor(s) (fixed effect(s)) and their potential interactions, and by adding a random effect of sites and season (1/site and 1/month), each one with 12 random-effect levels (i.e. 12 sites and 12 months). Given the strongly unbalanced datasets, potential interactions were not taken into account in order to facilitate model convergence and optimize the stability of models. The error distribution of each response variable was chosen after drawing a Cullen and Frey graph using the 'fidistrplus' package (Delignette-Muller and Dutang, 2015) and by fitting the resulting proposed distribution using the package 'gamlss' (Rigby and Stasinopoulos, 2005). All tools converged for each model towards the use of a beta distribution.

Logit was chosen as the link function. Before choosing the final model, i.e. the model having the lowest Akaike information criterion (AIC) values and being the most simplified as possible, random effect structure was tested, and then, simplified as far as possible by keeping only the significant random effects via the likelihood ratio test using the 'stats' R package. Any final model chosen was checked for validation using the DHARMA package (Hartig, 2018) by examining the Q-Q plot of overall deviations from the expected distribution (with supplementary tests for uniformity and outliers), and by examining residual plots including quantile regression lines (0.25, 0.5 and 0.75). Although testing for phylogeny signal in the residuals of the GLMMs to correct for potential autocorrelation/pseudo-replication, some 33% of copepod species had an unresolved genome (<http://lifemap-ncbi.univ-lyon1.fr/>, Table A3), preventing the building of an accurate phylogeny tree. Finally, goodness-of-fit of the models was assessed by calculating the Nakagawa's marginal and conditional *r*<sup>2</sup> (Nakagawa et al., 2017) using the 'performance' package (Lüdecke et al., 2019). GLMM analyses were performed using the 'glmmTMB' package (Brooks et al., 2017). Confidence intervals of fixed effect were calculated using the 'ggeffects' package (Lüdecke, 2018).

### 3. Results

#### 3.1. Environmental context and copepod community structure

The Chl *a* gradient across coastal waters of the Mediterranean Sea used in this study ranged from 0.11 to 17.3 µg Chl *a*/L, including some

well-known eutrophication hotspots such as the Nile delta, Gulf of Gabes, and Northern Adriatic Sea (Micheli et al., 2013). Salinity and temperature ranged from 29.4 to 41.5 and 9.5 to 30.3 °C, respectively.

Total copepod abundance was significantly different between sites (Kruskal-Wallis chi-squared = 68.25, p-value = 0). However, these differences did not always follow the Chl *a* pattern. For instance, the highest Chl *a* concentrations recorded at the Egypt CW site were accompanied by one to two orders of magnitude lower copepod abundances compared to other eutrophicated sites (N Adriatic Sea and Gulf of Gabes). This same Egypt CW showed copepod abundances of the same order as the low Chl *a* concentrations sites of the N Aegean Sea and Morocco.

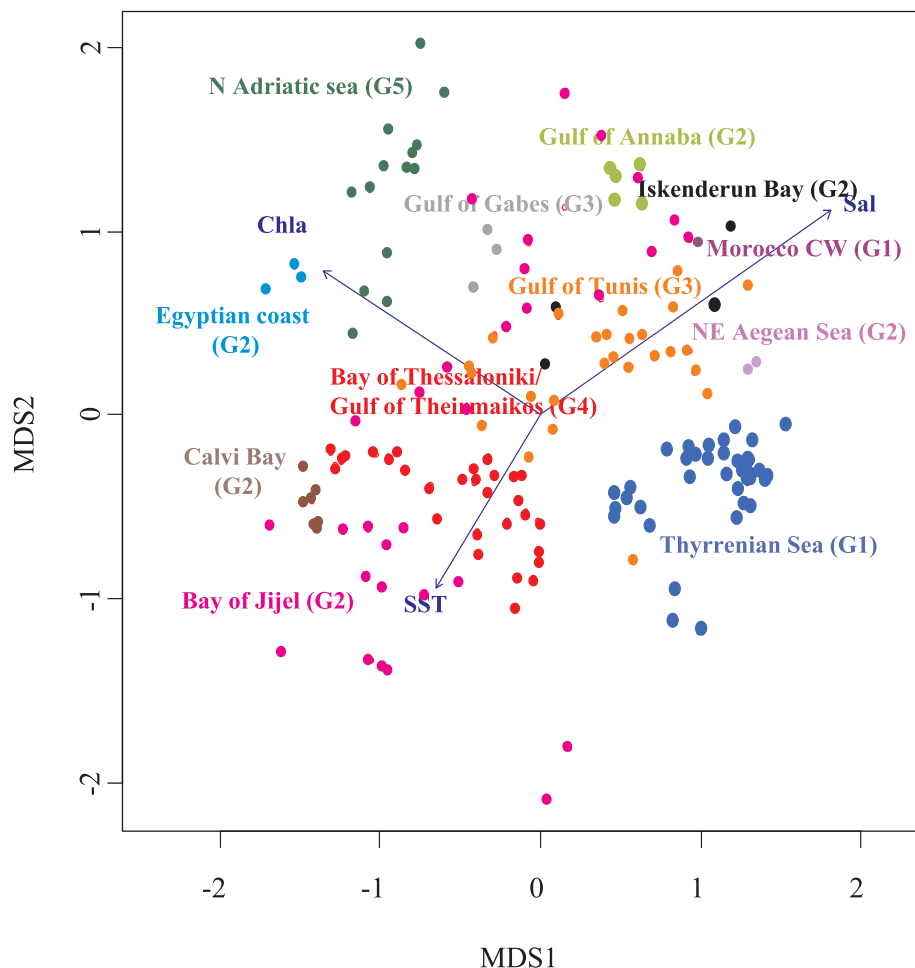
The nMDS results ( $p = 0.001$ , stress = 0.23) showed that the copepod community structure was dissimilar between the investigated Mediterranean sites. The adonis post-hoc test allowed to discriminating five different groups of sites in copepod species composition: (1) Thyrrenian sea and Morocco CW, (2) Bay of Jijel, Gulf of Annaba, Egyptian coast, Iskenderun Bay, N Aegean Sea, and Calvi Bay, (3) Gulf of Gabes and Gulf of Tunis, (4) Bay of Thessaloniki/Gulf of Theirmaikos, and (5) N Adriatic Sea. Except for group 3, sites were not associated in function of their geographical proximity (Fig. 2). Differences in copepod species composition was associated mostly to SST, salinity, and Chl *a*, which were significantly correlated to MDS1 or MDS2 ( $r^2 = 0.11$ ,  $p = 0.001$ ,  $r^2 = 0.16$ ,  $p = 0.001$ , and  $r^2 = 0.09$ ,  $p = 0.001$ , respectively). Accordingly, copepod composition in the N Adriatic Sea was associated to high Chl *a* but low salinity, while in

Morocco CW and the Thyrrenian Sea, Chl *a* was low but salinity high. Finally, for group 2, copepod species composition was not always associated to any particular amount of Chl *a*, salinity, and/or SST conditions.

### 3.2. Functional identity, trophic homogenization and functional diversity of the copepod community

The CWMs of feeding mode and ambush feeding strategy exhibited significant differences between groups of sites (Table 3). Accordingly, copepods exhibited mainly a passive mode in sites with the highest Chl *a* (group 5, some of group 2 including the Nile delta, and at some seasons in group 4), but an active one in sites with the lowest Chl *a* (group 1, half of group 2; the Gulf of Annaba, Morocco CW, and the NE Aegean Sea), with group 3 showing intermediary values. Moreover, copepods with an ambush strategy were more abundant in groups 5, some in group 2, and at some seasons in group 4. This was followed by group 3, group 1, and half of group 2 - which showed intermediary feeding mode values. Finally, CSI-trophic regime and CSI-feeding mode exhibited significant differences between stations/sites (K-W,  $p < 0.01$ ). Hence, values of CSI-feeding mode were significantly lower in sites having the highest Chl *a* values (group 5) than in the other groups, and values of CSI-trophic regime decreased from the sites having the lowest Chl *a* to those with the highest Chl *a* concentrations.

Furthermore, GLMM modelling showed significant relationships between Chl *a* and CWMs of feeding mode, ambush strategy, and CSI-



**Fig. 2.** Non-metric Multidimensional Scaling based on Bray-Curtis similarity (stress: 0.23) performed on the abundance of copepod species within the 162 communities (circles) sampled in coastal waters of the Mediterranean Sea. The five different groups of sites (G1-G5) depicted by ADONIS post-hoc test are between brackets. Salinity (Sal) was significantly linked ( $r^2 = 0.16$ ,  $p = 0.001$ ) to MDS1 while SST and Chl *a* were significantly linked to MDS2 ( $r^2 = 0.11$ ,  $p = 0.001$  and  $r^2 = 0.09$ ,  $p = 0.001$ , respectively).

**Table 3**

Significant generalized linear mixed models for community-weighted-means (CWM) of trait values for feeding modes, ambush feeding strategy, and Community Specialization Index of trophic regime (CSI-Trophic regime). Bold values indicating significant relationships ( $p < 0.05$ ) are those of the full model. All the models were built with a beta error distribution and a logit link.

	Estimate	SE	z value	p
<i>CWM-Feeding mode</i>				
(Intercept)	0.32	1	0.32	ns
Chla	<b>-0.08</b>	<b>0.02</b>	<b>-3.94</b>	<b>8.27E-05</b>
Sal	0.02	0.02	0.77	ns
SST	-0.005	0.01	-0.33	ns
Net mesh size	0.004	0.002	2.39	<b>0.0167</b>
random effect		variance	SD	
Site		0.06	0.25	
Season		0.06	0.24	
<i>CWM-Ambush feeding</i>				
(Intercept)	-0.64	1.05	-0.61	ns
Chla	0.08	0.02	4.19	<b>2.78E-05</b>
Sal	-0.01	0.03	-0.53	ns
SST	0.002	0.01	0.17	ns
Net mesh size	-0.003	0.002	-1.98	<b>0.0478</b>
random effect		variance	SD	
Site		0.05	0.23	
Season		0.05	0.23	
<i>CWM-CSI trophic regime</i>				
(Intercept)	-0.15	0.58	-0.26	ns
Chla	-0.06	0.01	-5.09	<b>3.61E-07</b>
Sal	-0.01	0.01	-0.74	ns
SST	-0.002	0.009	-0.22	ns
Net mesh size	0.002	0.001	1.38	ns
random effect		variance	SD	
Site		0.03	0.16	
Season		0.02	0.13	

trophic regime (Fig. 3, Table 3). Accordingly, copepod assemblages shifted towards the dominance of generalists using passive mode and ambush feeding strategy (Fig. 3). Given their significant relationship with Chl *a*, these traits were therefore considered as functional. All these traits were used for the calculation of functional dispersion (FDIs). However, results showed that FDIs did not follow the Chl *a* gradient for all functional traits used. Results from the analysis performed to identify the possible error distribution and diagnose residual of each significant GLMM model are given in Figs S2, S3, and S4.

#### 4. Discussion

The upscaling of original and existing data in the Mediterranean Sea, which included eutrophication hotspots such as the Nile delta, the Gulf of Gabes, and the Northern Adriatic Sea (Micheli et al., 2013), was conducted to explore how copepod assemblages responded to a Chl *a* gradient across coastal waters of the Mediterranean Sea. It also tested whether different functional indicators of copepod communities were associated with this gradient. Our results showed that eutrophication may lead to directional changes in the functional structure of copepod communities including trophic homogenization by favoring generalist against specialist feeders. To our knowledge, this is the first study documenting biotic homogenization within the copepod community as a result of eutrophication. Copepods play a pivotal role in the food webs and they are relatively easy to collect. Monitoring copepods could be of great importance in evaluating water quality and as a potential warning signal of the eutrophication phenomena. Our results have shown the effectiveness of applying a trait-based approach to copepods as a tool to detect early signal of eutrophication.

##### 4.1. Trait response and trophic homogenization of the copepod community to increasing chlorophyll *a*

Our results have shown that omnivorous copepods using a passive

mode and an ambush feeding strategy were favored as Chl *a* increased. Given that these traits typically characterize the cyclopoids of the genus *Oithona* (Benedetti et al., 2016), our results are in accordance with previous studies that have focused on species identity (e.g. Chang et al., 2009; Gao et al., 2019; Serranito et al., 2016; Sriwoon et al., 2008; Uye, 1994).

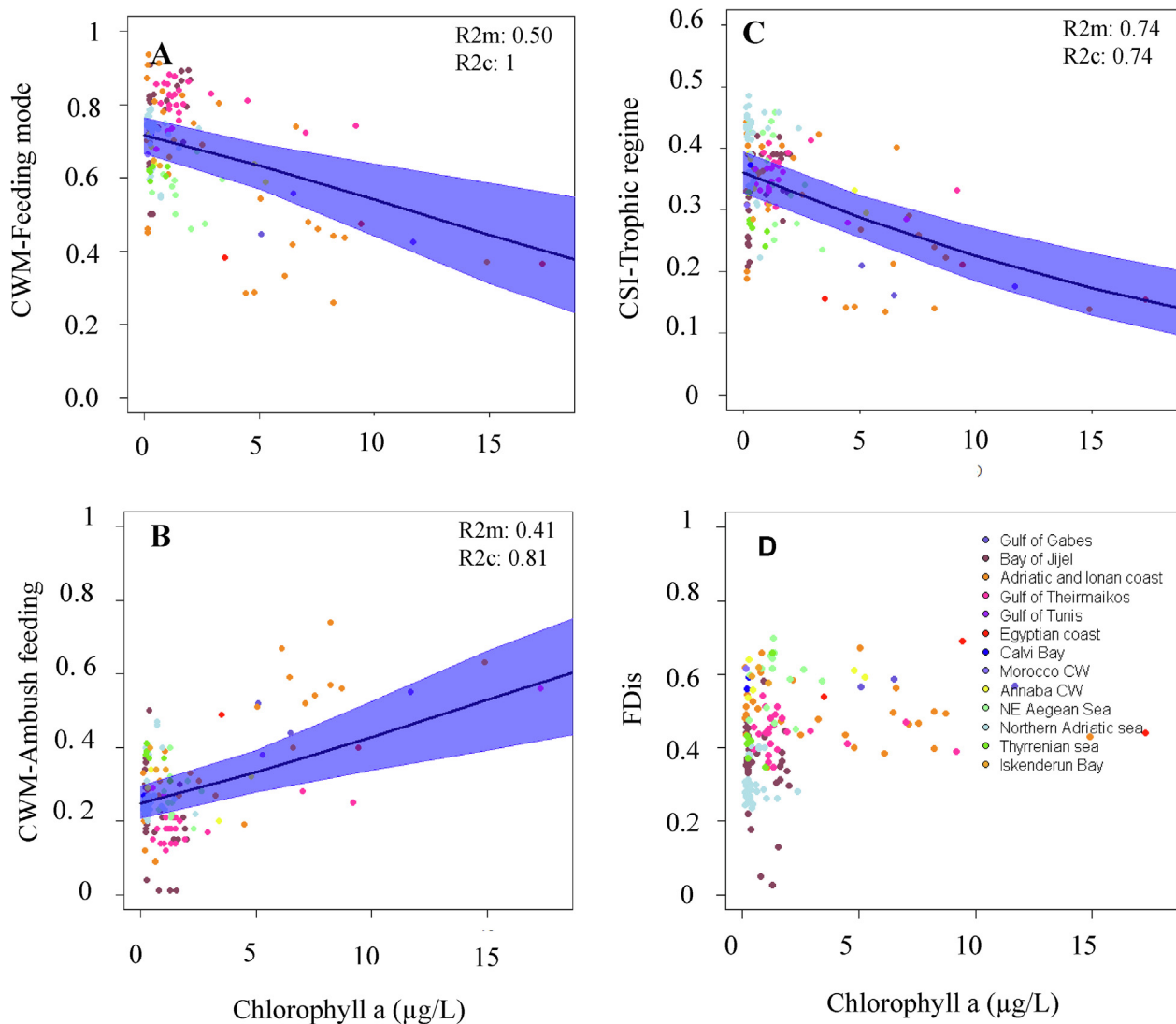
Several hypotheses have been advanced to explain why the genus *Oithona* is favored under eutrophic conditions including a shift in the food web structure (Uye, 1994; Sriwoon et al., 2008). Given the inverse relationship we found between the degree of resource specialization of the copepod community and Chl *a*, our results suggest a different story, i.e. the success of *Oithona* in eutrophicated environment is mainly due to its capacity to better adapt to a changing environment than other copepods. Generalists feed on many kinds of prey, and consequently, are less affected by the temporal variations of resources. *Oithona* spp. are typical ecological generalists (Paffenhöfer, 1993; Benedetti et al., 2016), and therefore, able to adapt to disturbed environments, eutrophicated systems, and unstable environmental conditions (Hautier et al., 2009; Hautier et al., 2015; Blüthgen et al., 2016; Pálffy and Vörös, 2019). Although *Oithona* spp. are poor competitors due to their relative inefficiency at capturing both non-motile and motile preys compared to active feeders (Kiørboe, 2011; van Someren Greve et al., 2017), they are able to switch from motile prey to non-motile phytoplankton, such as diatoms, when their preferred prey of ciliates and dinoflagellates are scarce (Castellani et al., 2005; Pond and Ward, 2011).

The lack of relationship between TL and Chl *a* should be considered with caution. Size data encompassed a relatively large geographical scale which is not necessarily representative to a restricted studied region. Size is considered as the 'master trait' for resource acquisition, reproduction, and predator avoidance (Litchman and Klausmeier, 2008). However, TL may not be responsive to eutrophication gradient because of an insufficient knowledge about copepod species size. Several of the studies used here have reported a directional change in size of the copepod community (e.g. Intxausti et al., 2012; Siokou-Frangou and Papathanassiou, 1991; Uye and Sano, 1998), but they have given no statistical evidence. Further studies are needed to clarify this point.

##### 4.2. Functional diversity and community assembly

No significant relationship was found between FDIs and Chl *a*. A decline in functional diversity under eutrophication has been observed in various ecological communities, including aquatic plants (Arthaud et al., 2012) and benthic macroinvertebrates (Zhang et al., 2019). This may result either from (i) environmental filtering, which under environmental stress selects species with the best-suited traits for survival (Weiher et al., 1998; Grime, 2006); either from (ii) strong competition resulting from the dominance of high competitive ability species (Mayfield and Levine, 2010); and/or (iii) predation by generalists, which are expected to cluster prey communities toward species having defense traits (Cavender-Bares et al., 2009). In our study, it is possible that opposite mechanisms driving copepod community assembly act simultaneously along the eutrophication gradient; consequently offsetting each other and resulting in the overall lack of change of FDIs to eutrophication gradient. Hence, by contrast to the different mechanisms cited above, competition based on the principle of limiting similarity (MacArthur and Levins, 1967) and predation by specialists may lead to trait over-dispersion (Cavender-Bares et al., 2009; Cornwell and Ackerly, 2009).

Our results showed also that specialists, i.e. the species with narrow ecological niches, are not necessarily functionally different from the others. This has also been observed by different authors in benthic invertebrates, butterflies, and forest birds (Larsen et al., 2018 and references therein). These authors suggest that while specialists and generalists have the same risk to extinct, specialists encounter some difficulty to recolonize a site.



**Fig. 3.** Significant relationships between community-weighted means (CWM) of trait values and Chl *a* according to GLMM analyses, taking into account random effect. (A) Feeding mode (active vs passive), (B) Ambush feeding strategy (C), and CSI-Trophic regime. Functional dispersion (D) is also displayed, while no significant relationship was found with Chl *a*. The blue line represents the overall trend. Filled area represents 95% confidence interval estimate for the slope of the regression. R2m and R2c are the marginal and conditional R2, respectively.

#### 4.3. Multiple indices to detect the effect of eutrophication on the biological organization of copepod communities

In our study, three indices from a total of six showed significant relationships with Chl *a* emphasizing the need to use multiple indices to give a chance to detect the effect of disturbance on copepod communities. Yet, our results showed clearly that the community composition changed between sites, which led to changes both in functional trait composition, and degree of specialization for resource of the copepod community. Although taxonomical-based diversity indices are widely used under the context of the EU Water Directive and the Marine Strategy Framework Directive (EU MSFD) to assess the ecological status of marine waters (Birk et al., 2012), the present study has shown that functional diversity indices may give insights when exploring the effect of environmental change on biodiversity.

## 5. Conclusion

Besides changes in community composition, we have shown that eutrophication may drive changes in the functional trait composition of the marine copepod community and alter the ratio between specialists

and generalists. Consequently, the use of multiple indices including trait-based ones are needed to give a chance to detect the consequence of eutrophication on the biological organization of the copepod community, and in general environmental changes in marine ecosystems. This study has shown that the trait-based approach is a powerful tool to help explore the biological organization of copepod communities in response to anthropogenic stress and copepods as cost-effective indicator of the environmental quality. Further studies on copepod monitoring and laboratory experiments to better define copepod species traits will help us to better understand the effect of anthropogenic activities on marine ecosystems.

#### CRediT authorship contribution statement

**Somia Chihoub:** Investigation, Methodology, Data curation, Writing - original draft, Writing - review & editing. **Urania Christaki:** Writing - original draft, Writing - review & editing. **Somia Chelgham:** Investigation. **Rachid Amara:** Project administration. **Zouhir Ramdane:** Investigation, Resources, Supervision, Project administration, Funding acquisition. **Aicha Zebboudj:** Investigation, Resources, Supervision, Project administration, Funding acquisition. **Sara Rachik:**



Investigation, Data curation. **Elsa Breton:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Writing - review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106388>.

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