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To cite this version:
Fabio Benedetti, Stéphane Gasparini, Sakina-Dorothée Ayata. Identifying copepod functional groups from species functional traits. Journal of Plankton Research, Oxford University Press (OUP), 2015, 38 (1), pp.159-166. 10.1093/plankt/fbv096 . hal-01296657

HAL Id: hal-01296657
https://hal.sorbonne-universite.fr/hal-01296657
Submitted on 1 Apr 2016

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SHORT COMMUNICATION

Identifying copepod functional groups from species functional traits

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Received June 15, 2015; accepted October 13, 2015

Corresponding editor: Roger Harris

We gathered information on the functional traits of the most representative copepod species in the Mediterranean Sea. Our database includes 191 species described by 7 traits encompassing diverse ecological functions: minimal and maximal body length, trophic group, feeding type, spawning strategy, diel vertical migration and vertical habitat. Cluster analysis in the functional trait space revealed that Mediterranean copepods can be separated into groups with distinct ecological roles.

KEYWORDS: copepods; functional trait; zooplankton; Mediterranean Sea

Functional traits are phenotypic characteristics of organisms that impact their fitness and are relevant to ecosystem function (Violle et al., 2007). For zooplankton, traits can be classified according to ecological functions—feeding, growth/reproduction, survival—and types—morphological, physiological, behavioural, life history (Litchman et al., 2013). As organisms have to allocate energy among ecological functions, traits relate to one another through trade-offs (Kiorboe et al., 2015). Litchman et al. (Litchman et al., 2013) recently advocated the implementation of a comprehensive matrix of key functional traits for zooplankton taxa. However, these functional traits have mainly been documented from laboratory experiments, thereby only encompassing a small number of species (Barnett et al., 2007; Saiz and Calbet, 2007; Barton et al., 2013; Kiorboe et al., 2015). For application in marine ecology, traits are needed at the species level and for the largest possible number of species, which requires the gathering of a huge amount of specific information. Such a challenge should be tackled step by step, focusing on some taxa and/or ocean basins at first. Functional traits could be used to gather species with
similar traits into functional groups (i.e. sets of species with similar effects on ecosystem functions and/or similar response to environmental conditions; Gitay and Noble, 1997) or to describe functional diversity of zooplankton communities (Barnett et al., 2007; Vogt et al., 2013; Pomerleau et al., 2015). Identifying and describing zooplankton functional groups should then increase our understanding of zooplankton ecological roles in marine ecosystems.

In this study, we developed a trait database for the most commonly sampled and abundant Mediterranean copepod species. Copepods are abundant in marine pelagic ecosystems (e.g. Siokou-Frangou et al., 2010) where they constitute the main trophic link between primary producers and higher trophic levels, such as small pelagic fishes (Costalago et al., 2015). Copepods are also relatively well documented in terms of distribution and biology (Razouls et al., 2005–2015). From this trait database, the aim of this study was to estimate how many functional groups could be identified among Mediterranean copepods, to characterize them and to discuss their ecological significance.

We considered 191 copepod species (Table I) that are the most representative of the Mediterranean copepod communities, in terms of both abundance and presence (Siokou-Frangou et al., 2010; Mazzochi et al., 2014). More details on how this list of species has been gathered are available in Supplementary data, Material S1. We used the following traits covering various types and ecological functions (Litchman et al., 2013), known to be ecologically meaningful (Kiorboe and Sabatini, 1994; Kiorboe, 2011; Kiorboe et al., 2015) and commonly used for zooplankton (Barnett et al., 2007; Barton et al., 2013; Pomerleau et al., 2015):

- two morphological traits which relate to many ecological traits: minimum and maximum adult body (cephalothorax) length (mm);
- one physiological trait defining the species’ trophic group (Carnivore, Omnivore–Carnivore, Omnivore, Omnivore–Herbivore, Omnivore–Detritivore);
- one behavioural trait depicting feeding strategy, classified into three classes (Kiorboe, 2011): active ambush feeding, cruise feeding and filter feeding, mixed feeding (for species that can switch between the three strategies);
- one life history trait related to reproduction, defining the egg-spawning strategy (broadcast-spawner, sac-spawner);
- one behavioural trait related to diel vertical migration (DVM) behaviour, classified into four classes according to the intensity of the observed migration: Non-migrant, Weak migrant (DVM occurs within tens of metres), Strong migrant (over several hundreds of metres), Reverse migrant (for species that migrate deeper at night).

All body sizes were obtained from Razouls et al. (Razouls et al., 2005–2015), whereas the other traits were obtained from an extensive literature review (see Supplementary data, Material S4 and Table SII for the full list of references). Additionally, to discuss the potential role of each functional group in the pelagic ecosystem, the species’ preferential depth layer was established (epi-/meso-/bathypelagic). We were able to determine at least 5 of the 7 functional traits for 171 species. The trait database for the 191 copepod species is available as Supplementary Table SII and can also be downloaded from PANGAEA (http://doi.pangaea.de/10.1594/PANGAEA.854331).

In order to identify functional groups, we performed a multiple correspondence analysis (MCA) on the trait matrix. MCA is an ordination method in reduced space for the multivariate analysis of categorical variables (Husson et al., 2010). The computation of the MCA functional space was performed on four traits: class of maximum body length (Size_1: 0.50–1.80 mm, Size_2: 1.89–2.85 mm, Size_3: 3.00–5.70 mm, Size_4: 6.10–11.0 mm), binary trophic group (Carnivore, Omnivore, Herbivore, Detritivore), feeding type and spawning strategy. Indeed, the minimum body length was highly correlated to the maximum body length ($R^2 = 0.866$, $n = 191$) and DVM behaviour was not taken into account since it tends to be very plastic for most species, meaning that it is known to vary greatly according to the environmental fluctuations and species’ ontogeny (see Pomerleau et al., 2015). A preliminary MCA incorporating these traits showed they had no impact in the definition of functional groups. Species for which the four traits were not fully defined were used as supplementary objects, meaning that they are associated with a group a posteriori, from their informed traits (see Supplementary data, Material S2 for more details on the MCA). The Euclidean distance among the 191 species in the functional space was computed using their coordinates along the four significant axes of the MCA (70.77% of the variance). Hierarchical agglomerative clustering was performed on this distance matrix using a synoptic aggregation method (Ward’s; Husson et al., 2010). Depending on the cutting level, two, three or six clusters could be identified (Fig. 1). The first level distinguished species according to the trophic group (carnivore vs. non-carnivore). Among non-carnivore species, the second level separated broadcasters from sac-splawners. Then, each of these groups was divided into two subgroups with different size and/or feeding type. Since higher cut levels could not be clearly related to functional traits, six functional groups were retained (Tables I and II). We will now detail each functional group and discuss their ecological role in the Mediterranean pelagic food web.
**Table I: List of the 191 Mediterranean copepod species whose traits have been described**

| Number | Species                        | 1 | 2 | 3 | 4 | 5 | 6 |
|-------|--------------------------------|---|---|---|---|---|---|
| 5     | Aetideopsis armata             | 6 | 6 |   |   |   |   |
| 10    | Augaptilus longicaudatus       | 7 | 2 |   |   |   |   |
| 11    | Augaptilus spinifrons          | 29| 3 |   |   |   |   |
| 27    | Candacia armata                | 31| 4 |   |   |   |   |
| 28    | Candacia bipinnata             | 34| 9 |   |   |   |   |
| 30    | Candacia ethiopica             | 35| 37|   |   |   |   |
| 32    | Candacia longimana             | 36| 38|   |   |   |   |
| 33    | Candacia norvegica             | 56| 39|   |   |   |   |
| 54    | Copilia quadrate               | 57| 40|   |   |   |   |
| 75    | Euchaeta acuta                 | 58| 41|   |   |   |   |
| 76    | Euchaeta marina                | 59| 42|   |   |   |   |
| 77    | Euchaeta media                 | 60| 43|   |   |   |   |
| 78    | Euchaeta spinosa               | 61| 44|   |   |   |   |
| 86    | Haloptilus acutifrons          | 62| 45|   |   |   |   |
| 87    | Haloptilus angusticeps         | 63| 46|   |   |   |   |
| 89    | Haloptilus mucronatus          | 64| 47|   |   |   |   |
| 90    | Haloptilus ornatus             | 65| 48|   |   |   |   |
| 91    | Haloptilus oxycephalus         | 66| 49|   |   |   |   |
| 92    | Haloptilus tenuis              | 67| 50|   |   |   |   |
| 93    | Heterorhabdus abyssalis        | 72| 51|   |   |   |   |
| 95    | Heterorhabdus spinifrons       | 83| 52|   |   |   |   |
| 143   | Paraechueta hebes              | 84| 53|   |   |   |   |
| 144   | Paraechueta norvegica          | 88| 54|   |   |   |   |

Continued
Table I: Continued

| Functional group | 1 | 2 | 3 | 4 | 5 | 6 |
|------------------|---|---|---|---|---|---|
| Number Species   | Number Species | Number Species | Number Species | Number Species | Number Species | Number Species |
| 147  Phaenna spinifera  | 94  Heterorhabdus papilliger | 74  Eucalanus hyalinus | 136  Oncaea venusta |
| 158  Sapphirina angusta  | 99  Lubbockia aculeata | 98  Labidocera wollastoni | 137  Oncaea waldeirensis |
| 160  Sapphirina gemma | 100  Lubbockia squilliman | 101  Lucicuta clausi | 142  Paracalanus latisetos |
| 161  Sapphirina intestinata | 138  Pachos punctatum | 102  Lucicuta flavicoreis | 155  Pseudocalanus elongatus |
| 163  Sapphirina metalilia | 145  Parapontella brevicornis | 103  Lucicuta gaussae | 170  Scaphocalanus curtis |
| 164  Sapphirina nigromaculata | 153  Pontellina plumata | 104  Lucicuta gemina | 171  Scaphocalanus invalidus |
| 165  Sapphirina opalina | 154  Pontellopsis villosa | 105  Lucicuta ovalis | 172  Scolecithricella abyssalis |
| 166  Sapphirina oseolaceolata | 159  Sapphirina aurontiens | 108  Mesocalanus tenicorhins | 173  Scolecithricella dentata |
| 167  Sapphirina sali | 162  Sapphirina lactens | 112  Monacilla typica | 174  Scolecithricella tenuiserrata |
| 168  Sapphirina scarlata | 169  Sapphirina vorax | 114  Mormonillia phasma | 175  Scolecithricella vittata |
| 115  Nannocalanus minor | 116  Neocalanus gracilis | 117  Neocalanus robustior | 176  Scolecithrix bradyi |
| 139  Paracalanus denudatus | 130  Paracalanus nanus | 139  Paracalanus parvus | 177  Scolecithrix danae |
| 140  Paracalanus lonchicor | 141  Paracalanus parvus | 146  Paracalanus attenuatus | 178  Spinocalanus abyssalis |
| 148  Pleuromamma abdominalis | 149  Pleuromamma borealis | 148  Pleuromamma gracilis | 179  Spinocalanus longicornis |
| 150  Pleuromamma gracilis | 151  Pleuromamma xiphias | 152  Pontella mediterranea | 183  Triciona conifera |
| 156  Rhincalanus cornutus | 157  Rhincalanus nasutus | 160  Subeucalanus crassus | 184  Triciona dentipes |
| 180  Subeucalanus monachus | 181  Subeucalanus monachus | 182  Temora stygia |

The species are numbered by alphabetical order but gathered by functional groups, as revealed by the hierarchical clustering on the first four axes of the MCA on functional traits (see Fig. 1). The species with bold numbers are the 99 species used in the MCA space calculation.
Group 1 is composed of large carnivores that primarily feed by cruising. There is no unique reproductive strategy, though the species are mainly sac-spawners. Many species have a broad vertical distribution, ranging from the epipelagic to the bathypelagic. Representative genera are Calanoids such as *Candacia* spp., *Haloptilus* spp., *Heterorhabdus* spp., members of the Euchaetidae family and Cyclopoids of the *Sapphirina* genus. These species are known to prey on smaller copepods, as well as other zooplanktonic taxa, such as doliolids (Takahashi et al., 2013), larvaceans (Ohtsuka and Onbé, 1989) and even fish larvae (Yen, 1987).

Group 2 is defined by smaller carnivore species, all active ambush feeders and mainly sac-spawners, belonging to the Corycaeidae family. These are small visual predators that prey on nanoplanktonic taxa, such as doliolids (Takahashi et al., 2013), larvaceans (Ohtsuka and Onbé, 1989) and even fish larvae (Yen, 1987).

Group 3 gathers a lesser number of species and consists of Calanoids of the genera *Centropages* and *Acartia*. They are small omnivorous broadcasters, but phytoplankton can become an important component of their diet. They exhibit mixed feeding strategies, depending on the available food items. *Acartia* spp. and *Centropages* spp. are generally restricted to the epipelagic and are affiliated with neritic environments (Siokou-Frangou et al., 2010).

Group 4 is the largest group and comprises almost all filter-feeding species, spanning all size classes, with a clear tendency towards herbivory. The species of this group for which reproductive strategy could be found were mainly broadcasters. This group contains not only small-bodied calanoids that are numerically very important in the Mediterranean epipelagic (*Clausocalanus* spp., *Calocalanus* spp., *Temora stylifera*; Mazzocchi et al., 2014), but also larger calanoids, some of which are strong vertical migrants, such as *Calanus helgolandicus*, *Pleuromamma* spp. or *Neocalanus* spp. (Andersen et al., 2001, 2004). The small surface calanoids are the target prey for larval and juvenile pelagic fish (Borne et al., 2013; Costalago et al., 2015), whereas larger calanoids are the preferential prey of Mediterranean mesopelagic fishes (Palma, 1990). Additionally, the strong calanoid migrants might play a differential key role in carbon cycling as they graze upon microalgae in the euphotic zone, and then migrate below the permanent thermocline where they excrete their lipid reserves (lipid pump hypothesis; Jónasdóttir et al., 2015). Therefore, Groups 3 and 4 are crucial for the transfer of energy from photoautotrophs to higher trophic levels, both in neritic (Group 3) and in oceanic environments (Group 4). Also, the latter group might comprise species that play a potentially underestimated role for the carbon flux (Jónasdóttir et al., 2015).

Group 5 consists essentially of *Oithona* spp. These are small active ambush-feeding omnivores that carry their
eggs. It is difficult to assign a particular ecological function to such a group, since *Oithona* spp. are a major component of the global ocean’s plankton, independently of environmental conditions (Gallienne and Robins, 2001). Feeding and trophic group were unknown for the other species of Group 5. Therefore, they are related to *Oithona* spp. only because they are small (<1.8 mm) sac-spawners. Group 6 also comprised small sac-spawning omnivores, but these are mainly cruising detritivores (*Oncaea* spp., *Microsetella* spp.) or herbivores (*Clausocalanus* spp.). The former usually exhibit a wide vertical distribution, while the latter are epipelagic. *Oncaea* spp. and *Microsetella* spp. are known associates of appendicularian houses (Alldredge, 1972; Steinberg et al., 1994). Several calanoid species of this group (*Euchirella* spp., Scolecitrichidae) are also deep-water detritivores. Consequently (and as suggested by a higher cut level on dendrogram Fig. 1), Group 6 could be sensibly divided into two subgroups: (i) deep-water dwelling detritivores that actively participate in the recycling of particulate organic matter and (ii) small cruising grazers contributing to epipelagic secondary production.

By focusing on Mediterranean copepods, we were able to gather information on functional traits for 191 species, with at least 6 traits described for 135 species and 7 for 66 species. Using 4 of these traits, functional groups with different ecological roles were described. Although the definition of these groups was robust (similar groups were found using a K-means partitioning method, or accounting for all traits), the main limitation, as for any trait-based approach, remains the scarcity of trait descriptions at the species level. Compiling a trait database for a larger number of zooplankton species remains challenging, but the present initiative demonstrates the usefulness of this endeavour.

The present study also confirmed or revealed trade-offs among zooplankton functional traits (Litchman et al., 2013, Kiorboe, 2011). For instance, small carnivores and small omnivores were active ambush feeders, while large

| Functional trait | Category | Group 1 | Group 2 | Group 3 | Group 4 | Group 5 | Group 6 | Total number of species |
|------------------|----------|---------|---------|---------|---------|---------|---------|------------------------|
| Class of maximum body length | Size_1 (0.50–1.80 mm) | 0 | 12 | 6 | 16 | 20 | 32 | 98 |
| | Size_2 (1.89–2.85 mm) | 0 | 20 | 6 | 17 | 0 | 8 | 51 |
| | Size_3 (3.00–5.70 mm) | 30 | 1 | 0 | 10 | 0 | 1 | 42 |
| | Size_4 (6.10–11.0 mm) | 3 | 0 | 0 | 7 | 0 | 2 | 12 |
| Trophic group | Carnivore | 25 | 29 | 0 | 0 | 0 | 0 | 54 |
| | Omnivore | 0 | 0 | 6 | 12 | 11 | 4 | 33 |
| | Omnivore–carnivore | 6 | 1 | 1 | 0 | 0 | 0 | 8 |
| | Omnivore–detritivore | 0 | 0 | 0 | 0 | 0 | 28 | 28 |
| | Omnivore–herbivore | 0 | 0 | 4 | 36 | 0 | 11 | 51 |
| | NA | 2 | 3 | 1 | 2 | 9 | 0 | 17 |
| Feeding type | Active ambush | 0 | 16 | 0 | 0 | 11 | 1 | 28 |
| | Cruise | 11 | 5 | 0 | 3 | 0 | 15 | 34 |
| | Filter | 4 | 0 | 0 | 43 | 0 | 8 | 55 |
| | Mixed | 0 | 0 | 11 | 0 | 0 | 2 | 13 |
| | NA | 18 | 12 | 1 | 4 | 9 | 17 | 61 |
| Spawning strategy | Broadcaster | 7 | 7 | 11 | 24 | 0 | 3 | 52 |
| | Sac-spawner | 16 | 20 | 0 | 3 | 17 | 28 | 84 |
| | NA | 10 | 6 | 1 | 23 | 3 | 12 | 55 |
| Type of DVM | No DVM | 13 | 8 | 6 | 13 | 2 | 15 | 57 |
| | Weak DVM | 0 | 1 | 0 | 0 | 2 | 2 | 5 |
| | Strong DVM | 2 | 1 | 0 | 8 | 0 | 2 | 13 |
| | Reverse DVM | 5 | 12 | 2 | 15 | 2 | 14 | 50 |
| | NA | 13 | 11 | 4 | 14 | 4 | 10 | 66 |
| Vertical distribution | Epipelagic (0–200 m) | 10 | 2 | 11 | 21 | 7 | 14 | 65 |
| | Epimesopelagic (0–1000 m) | 11 | 14 | 0 | 17 | 7 | 13 | 62 |
| | Epibathypelagic (0–4000 m) | 11 | 15 | 0 | 9 | 2 | 9 | 46 |
| | Mesopelagic (200–1000 m) | 0 | 1 | 0 | 0 | 0 | 2 | 3 |
| | Mesobathypelagic (200–4000 m) | 1 | 0 | 1 | 3 | 2 | 4 | 11 |
| | NA | 0 | 1 | 0 | 0 | 2 | 1 | 4 |
| Mean minimum body length (mm) | 2.27 | 1.18 | 1.07 | 1.47 | 0.67 | 0.93 | – |
| Mean maximum body length (mm) | 4.47 | 2.03 | 1.82 | 2.95 | 1.11 | 1.74 | – |
| Total number of species | 33 | 33 | 12 | 50 | 20 | 43 | 191 |

The number of species recorded within each trait’s class and within each functional group is reported. The groups are based on hierarchical clustering on the first four axes of the MCA based on four functional traits: class of maximum body length, binary trophic group, feeding type and spawning strategy. For information, the type of DVM, the vertical distribution, the average minimum body length (mm) and the average maximum body length (mm) are also indicated (in grey).

NA, not available; DVM, diel vertical migration.
carnivores were cruise feeders. This relationship between size and feeding strategy could be explained by the differences in metabolic requirements. Indeed, whereas cruise feeders have to swim actively to encounter their prey, ambush feeders passively encounter them (Kiørboe, 2011), which requires less energy. As metabolic rates scale with body size (Kiørboe and Hirst, 2014), this difference in metabolic requirement could explain their difference in size. We also found that sac-spawners were active ambush feeders or cruise feeders, whereas broadcasters were mainly filter feeders or mixed feeders. This could be due to optimal resource allocation: egg-carrying ambush-feeding copepods have longer lifespans and lower fecundity rates than broadcasting active feeders (Kiørboe and Sabatini, 1994; Kiørboe et al., 2015). We also found that three quarters of the carnivorous species were sac-spawners; hence, these exhibit a higher degree of parental care and avoid predation on their own eggs. Conversely, for epipelagic omnivorous filter feeders, which are heavily preyed upon by other zooplankters and fishes, broadcasting is likely to be favoured to avoid being eaten together with the eggs, as an adaptation to the elevated mortality of ovigerous females (Kiørboe and Sabatini, 1994). Together, these results call for a better understanding of the mechanistic processes that lead to such trade-offs across traits.

The functional trait database compiled here can be used to estimate the functional diversity of zooplankton communities (Vogt et al., 2013; Pomerleau et al., 2015) and test whether traits can be related to environmental variables (Barton et al., 2013). Finally, the existence of several functional groups encourages the integration of more diverse planktonic assemblages in ecosystem models.

SUPPLEMENTARY DATA
Supplementary data can be found online at http://plankt.oxfordjournals.org.

DATA ARCHIVING
The trait database for the 191 copepod species can be downloaded from PANGAEA (http://doi.pangaea.de/10.1594/PANGAEA.854331).

ACKNOWLEDGEMENTS
The authors are grateful to Andrew Hirst (QMUL), Martine Fioroni (OOV) and Ruth Böttger-Schnack (GEOMAR) for their help in identifying additional references for compiling the specific trait database. We thank four anonymous reviewers for their helpful comments and suggestions for improving a previous version of the manuscript. We also thank Erin Cox and Martin Lilley for the English proofreading.

FUNDING
Financial support was provided by the EC FP7 PERSEUS Project (Grant. Agr. 287600), the MerMEx (Marine Ecosystems Response in the Mediterranean Experiment)/MISTRALS French National Program through the PlankMed action and the Climate-KIC of the European Institute of Innovation & Technology (EIT) through a PhD grant to EB. Funding to pay the Open Access publication charges for this article was provided by the EC FP7 PERSEUS Project.

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