

MEIOZORES 2019 - EXPLORING THE MARINE MEIOFAUNA OF THE AZORES

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ABSTRACT

In July 2019 an international team of 39 senior and junior researchers from nine countries met at the University of the Azores in Ponta Delgada, São Miguel for a 10-days

workshop/ summer school to explore the meiofaunal biodiversity in marine sediments of the Azores. In total, we sampled intertidal and subtidal sediments from 54 localities on 14 major sites around São Miguel and additionally explored eight freshwater and terrestrial sites for rotifers. We sorted and investigated more than 2000 living specimens in the field, yielding approximately 180 species of soft-bodied meiofauna, representing most major clades of meiofauna with a focus on nematodes, polychaete annelids, proseriate and rhabdocoel flatworms, gastrotrichs, acoelomorphs, nemerteans, molluscs and cnidarians. Most of the encountered diversity shows similarities to the North-East Atlantic continental meiofauna, but in-depth morphological and molecular analyses are still pending. About 60 of the 180 species could not be assigned a species-level identification in the field, and nearly 15% of the total diversity is expected to be new to science and is awaiting formal description. Herein, we present an overview of the results of the workshop, providing detailed information on the sampling sites, methodology and encountered diversity, and we offer a preliminary discussion on aspects of faunal elements shared with other biogeographic regions. We highlight the most common members of the marine meiofauna of the Azores, provide preliminary diversity estimates and suggest a roadmap for future research towards a better understanding of the meiofauna in this remote archipelago.

RESUMO

Em julho de 2019, uma equipa internacional de 39 investigadores seniores e juniores de nove países reuniu-se na Universidade dos Açores em Ponta Delgada, São Miguel, durante 10 dias, para um workshop /escola de verão com objectivo de explorar a biodiversidade da meiofauna em sedimentos marinhos dos Açores. No total, foram amostrados sedimentos intertidais e subtidais de 54 pontos em 14 locais ao redor de São Miguel. Adicionalmente, oito locais de água doce e terrestres foram explorados em busca de rotíferos. Classificámos e investigámos mais de 2 000 espécimes e estimámos preliminarmente uma diversidade de aprox. 180 espécies de meiofauna, representando a maioria dos principais grupos de meiofauna eg. nematodes, anélidos poliquetas, vermes achatados proseriados e rhabdocelos, gastrotríquios, acelos e nematodermatídeos, nemertíneos, moluscos e cnidários. A diversidade encontrada mostra semelhanças com a meiofauna continental do Atlântico Nordeste, mas análises morfológicas e moleculares aprofundadas ainda estão pendentes. Quase um terço das espécies era indeterminável no campo, mas cerca de 15% das espécies encontradas serão novas para a ciência, aguardando descrição formal. Aqui apresentamos uma visão geral dos resultados do workshop fornecendo informações detalhadas sobre os locais de amostragem, metodologia, diversidade encontrada e discutimos aspectos preliminares sobre os elementos faunísticos comparando-os com outras regiões biogeográficas. Destacamos os membros mais comuns da meiofauna marinha dos Açores, fornecemos estimativas preliminares de diversidade e sugerimos um roteiro para investigações futuras com vista a proporcionar um melhor conhecimento da meiofauna neste arquipélago.

INTRODUCTION

The Azores form a remote oceanic archipelago in the North Atlantic comprising nine islands at 580 km distance to the nearest other oceanic island (Madeira) and almost 1300 km to the nearest continental land (Cabo Roca, Portugal). They are geologically young islands, which started surfacing in the

late Miocene about 6 mya (Ramalho *et al.*, 2017) by volcanism associated with the seafloor spreading of the Mid-Atlantic Ridge (Mitchell-Thomé, 1976). Oceanic islands, like the Azores, are often considered natural evolutionary laboratories (*e.g.*, Losos & Ricklefs, 2009), which attract the interest of taxonomists and evolutionary biologists worldwide with their unique faunas and floras and

high rates of endemism. A recent and ongoing inventory of Azorean biodiversity currently reports 8047 species constituting the Azorean fauna and flora, of which 411 are considered to be endemics, with most of those being terrestrial arthropods and molluscs (Borges *et al.*, 2010).

Exploration of the marine biodiversity of the Azores was greatly advanced through a series of international workshops under the patronage of the Sociedade Afonso Chaves and the University of the Azores, which started in 1988 with studies focused on the littoral and sublittoral of the Azorean coast (Martins, 2009). These and other local efforts to enhance the knowledge of the littoral marine biodiversity of the Azores have accumulated to date 1883 marine species in 16 phyla, with 39 of those species (mainly molluscs) considered to be putative endemics to the Azores (Borges *et al.* 2010). The marine component of Azorean biodiversity, currently constituting approximately 23% of the overall species diversity, is likely to be considerably undercounted as detailed inventories are lacking, especially for several major clades of marine invertebrates.

This deficiency is most evident when it comes to the marine meiofauna: meiofauna forms a size-defined group of animals, which pass through a 1 (or 0.5 mm, depending on definitions) mm sieve, while being retained in one of 63 μm (or 45 μm), and includes fauna living on benthic surfaces as well as within sediments (Higgins & Thiel, 1988; Giere, 2009). Meiofauna harbors representatives of almost all metazoan phyla and due to the spatial restrictions of the often infaunal habitat, marine

meiofauna includes aberrant free-living forms of several metazoan phyla. Their still poorly understood diversity continues to reveal new body plans decisive for our understanding of metazoan evolution (Worsaae & Rouse, 2008; Worsaae *et al.*, 2012; Laumer *et al.*, 2015). From an ecological perspective, meiofaunal activities can considerably affect sediment properties and therewith influence ecosystem services and food web dynamics (Schratzberger & Ingels, 2018) and it should thus not be neglected in ecological and conservational approaches, which rely on underlying biodiversity information.

In general, knowledge of meiofaunal diversity and biogeographic patterns is still patchy on a global scale, with many regions which are virtually unstudied. When (re-) investigated via joined meiofaunal workshops even shallow-water meiofaunal communities of the European Atlantic Coast and Mediterranean with a long tradition of meiofaunal research (*e.g.*, Swedmark, 1964; Coull & Giere, 1988) reveal a wealth of new species records for the respective country (Willems *et al.*, 2009) and still harbour up to 37% of species new to science (Curini-Galletti *et al.*, 2012). Remote oceanic islands are suspected to provide a depauperate meiofauna due to limited dispersal abilities usually attributed to most groups of marine meiofauna. But a first study on the patterns of diversity and endemism in marine soft-bodied meiofauna of the oceanic Canary islands surprisingly did not detect a significant effect of size of the specimens and the presence of dispersal stages on the number of endemic species and revealed a similar species diversity than in previous meiofaunal workshops in Sweden or Sardinia (Martínez *et al.*, 2019). Strikingly,

the proportion of specimens, which are indeterminable and likely present species new to science was much higher on the Canaries than in previous workshops in better-surveyed areas (Martínez *et al.*, 2019). This is comparable in the rate of discovery to a recent (smaller) meiofaunal inventory on Hawaii, which resulted in the collection of about 80 morphologically distinct species, of which at least 70 are likely to represent new species (JN, unpublished data).

So far, little is known on the infauna of marine sediments around the Azores and even less on the associated meiofauna (Morton *et al.*, 1998): Wells (1995) investigated the sediments of the lagoon of Ilhéu de Vila Franca do Campo, São Miguel and reported an impoverished infauna. This paucity of marine invertebrates concerning the diversity of species as well as abundance and biomass of the occurring species was also confirmed by Bamber & Robbins (2009), who sampled littoral and sublittoral sediments around Vila Franca do Campo, São Miguel, which were dominated by taxa that can tolerate unstable sediments. The authors attributed the low diversity to the sediment instability on the generally high-energy coast of the Azorean islands. Another explanation for the almost life-devoid sandy beaches in the Azores in present times has been postulated by Ávila *et al.* (2008), to be the lack of suitable habitat (sand) related to the sea-level drop during the last glaciation when a large portion of sand-associated organisms disappeared or went locally extinct.

Only a few scattered records exist on certain taxa of meiofauna from the

Azores (*e.g.* Kunz (1983) on harpacticoid copepods, Green (1992) reporting freshwater rotifers, Hummon, (2008;2010) on marine Gastrotricha, Klink *et al.* (2015) described an aplacophoran mollusc). A preliminary ecology study on the effects of the outlet emission of a wastewater treatment plant allowed addressing the local meiofauna community (see Álvaro *et al.*, 2001), revealing that this faunistic component comprises a more abundant and taxonomic richer soft-bottom community than its macrofaunal counterpart. The need and scientific interest for an extensive taxonomic approach to the study of meiofauna was unequivocally set.

The present summer school funded by the VW foundation (Germany) and the Government of the Azores combined the education of PhD students in the field to train a future generation of meiobenthologists with an exploratory biodiversity study of the local marine meiofauna, aiming to contribute to a better knowledge of the biodiversity of the Azores. Subgroups of taxonomists and students sorted, analyzed and documented the local Azorean meiofauna of the São Miguel coast to establish a baseline inventory of the local marine meiofauna. Here we present an overview on sampling sites, methodology and the general results of the encountered biodiversity, discussing trends in meiofaunal biodiversity, faunal overlaps with other regions and the rate of endemism.

MATERIAL AND METHODS

Sampling

The workshop “Meiozores2019 – Exploring the marine meiofauna of the Azores” was held for ten days

in June 2019 at the University of the Azores in Ponta Delgada, São Miguel, Azores. Due to the limited timeframe, the sampling focused on intertidal and shallow subtidal sediments of the coast of São Miguel. We sampled a variety of intertidal sediments with different degrees of exposure to waves and different levels to the waterline, as well as subtidal sediments from the sandy bottom and sandy patches among the rocky shore. Additional small exploratory trips were conducted to sample freshwater and terrestrial habitats for Rotifera and some additional comparative sampling took place on Santa Maria Island after the workshop (see Curini-Galletti, 2021). In total, we took 54 sediment samples around 14 major sites around São Miguel, and additionally sampled eight freshwater and terrestrial stations (see Figure 1, description and coordinates of all samples are listed in Table 1). Intertidal samples were collected by hand, scooping the oxygenated top 5 cm layer of the sediments into buckets or jars; subtidal samples were collected either via snorkeling or by means of SCUBA diving. Each individual station was sub-sampled for granulometry and each major site was sub-sampled for metabarcoding (see below).

Extraction techniques

Samples were brought to the laboratory and processed either directly or after a 1-2 day resting period. Sediment samples were usually processed with a $MgCl_2$ -seawater decantation technique with sieves of 63 μm mesh size, or in parts via siphoning off the water above the sediment for qualitative analyses (Higgins & Thiel, 1988); no quantitative

extraction was performed. The extracted meiofauna was sorted into phyla of interest and all individuals were identified alive to the lowest possible taxonomic level, photo-documented and fixed for subsequent morphological or molecular analyses in the home labs of the participating senior scientist.

Sediment description and granulometry

Many beaches of the Azores consist of mobile cobble and boulders. Few sandy beaches and interspersed deposits of sediment and only rarely muddy silt can be found. Azorean sediments are largely derived from basaltic lava flows and ash falls, while limestone of biogenic origin is also represented in smaller quantities (Morton *et al.*, 1998). We took sediment samples from each station and analyzed the granulometry of one selected station per major site (unless major sites included stations with different grain sizes, *e.g.*, fine and medium coarse sand (see Table 1), then representative of both sediment types were analyzed) based on classified image analyses (following the methodology by Lira & Pina, 2009; Lira & Pina, 2011). Sediment samples were scanned at 1600 dpi in RGB colour and saved in tif.-format. Using Fiji based on ImageJ (Schneider *et al.*, 2012; Rasband, 2018), we first followed the steps of treatment and preparation of the image by i) transforming them in 8 bit, ii) reduction of the luminosity bias (PROCESS – FILTERS – MEAN), iii) segmentation to separate sediment particles in pixels (IMAGE – ADJUST – THRESHOLD), iv) filling holes created by distinct mineralogical crystallization (PROCESS – BINARY – FILL HOLES), and removing

the outliers (PROCESS – NOISE – REMOVE – OUTLIERS). Then, we measured the particles using the tool “ANALYZE – SET MEASURE” and “ANALYZE PARTICLES”. The diameter (D0) was used to transform all values of grains to the phi scale. The percentage and the histograms were obtained with the RYSGRAN package for R (Camargo, 2006) following the method of Folk & Ward (1957). Verbal classification of the sediment is based on Wentworth tables (Wentworth, 1922). Results are summarized in Table 2 and Figure 2.

Metabarcoding

A total of 15 subsamples were taken from intertidal sediment samples (Table 1) for inspecting the meiofaunal community through DNA metabarcoding. Approximately, 300 mL \pm 50 of sediments were collected in a beaker, to which isotonic MgCl₂ isotonic was filled up to 500 mL, and left to settle for about 5-7

minutes. Sediments were filtered for 3 times, using a 63 μ m mesh sieve. The retained fauna collected in the sieve was transferred into 50 mL Falcon tubes using 1 mL \pm 0.2 of double distilled water, and fixed with EtOH ~95% until reaching 50 mL. The metabarcoding subsamples were stored at 4 °C until the high throughput sequencing (HTS) analyzes. The results will be presented and discussed separately.

RESULTS

Overview of the encountered meiofaunal diversity

In total, we sampled and investigated over 2000 specimens targeting on soft-bodied meiofauna (but see Andrade *et al.*, 2021 on soft-bottom amphipods collected during this workshop). We report meiofaunal species diversity of approximately 180 species across ten phyla, based on preliminary data in the field, dominated



FIGURE 1. Map showing the localities of the sampling sites.

by the typically species-rich groups of Nematoda and Platyhelminthes. Due to the limited data available on the meiofauna of the Azores before the Meiozores2019 workshop, the vast majority of the encountered species diversity presents new records for the Azores and an estimated 15% of the encountered species diversity is likely new to science, awaiting formal description.

Among our meiofauna taxa in focus, nematodes formed the most species-rich clade with 43 different genera encountered and estimated species diversity of 65-70 species (see de Jesus-Navarrete *et al.*, 2021).

In total, we discovered 45 species of Platyhelminthes: 29 species of Rhabdocoela (i.e., 17 Eukalyptorhynchia, 3 Schizorhynchia, 7 Thalassotyphloplanida, 2 Neodalyellida), 24 species of Proseriata (see Curini-Galletti, 2021 for details) and one Tricladida and one Polycladida. At least 10 species of Proseriata and 13 Rhabdocoela are deemed new to science and potentially endemic to the Azores.

Twenty-one species of gastrotrichs were collected in the course of this survey and classified in 13 different genera (see Araújo & Hochberg, 2021). Surprisingly only one of twelve previously reported gastrotrich species from the Azores (Hummon, 2008; 2010) was recollected during the Meiozores2019 workshop. Remarkable is the finding of one specimen of *Megadasys* sp., which is 2.3 mm long and is one of the most giant gastrotrich species reported worldwide.

Interstitial annelids were locally common in the samples of the workshop and a total of 12 species of entirely interstitial families could be identified, belonging to Diurodrilidae,

Microphthalmidae, Nerillidae, Proto-drilidae, and Saccocirridae (see Martínez *et al.*, 2021). Out of these 12 species one is unequivocally new to science, whereas the status of the remaining 11 needs to be confirmed by further morphological and molecular analyses.

We recorded 14 species of Acoelomorpha based on 86 collected and documented specimens. Out of those 14 species, five are deemed new to science, the remaining species have been reported from the North-East Atlantic and/ or the Mediterranean (see Table 3 for details).

Interstitial molluscs were rare among the fauna documented during Meiozores2019 with five species of interstitial gastropods (with only six specimens collected in total) encountered, plus an additional nudibranch *Pseudovermis* sp. from Santa Maria (one specimen); one species of *Rhodope* and two species of *Hedylopsis* are new to science; *Pseudovermis* sp. requires further molecular and in-depth morphological analyses. The encountered species of caenogastropod Caecidae were previously known from the Azores, Canary Islands and the North-East Atlantic. We recorded four different morphospecies of Solenogastres, which were more common with 39 specimens in total, however only three are supported by preliminary barcoding data, two species are new to science, one was previously described from the Azores (see Neusser *et al.*, 2021, uniting the Meiozores2019 sampling data with those of a previous sampling trip in 2013).

Interstitial nemerteans were also rare: the sampling efforts resulted in eight species (approx. 50 specimens) identified based on

TABLE 1. Stations of Meiozores2019. Stations coordinates georeferenced with Google Earth maps (* marks coordinates referenced via GPS). Collectors: AM, Anna Mikhailina; AMG, Alejandro Martínez García; AS, Alexandra Savchenko; AZB, Andrea Zita Botelho; DF, Diego Fontaneto; DGF, Duarte G. Frades; FSB, Franziska S. Bergmeier; FG, Freya Goetz; IC, Irina Chemeva; JFP, Juan Carlos Farias Pardo; JN, Jon Norenburg; KMJ, Katharina M. Jønger; LT, Lenke Tödter; MD, Maikon Di Domeniko; NDS, Nuno da Silva Ascensão Vaz Alvaro; NL, Nina Lucas; TA, Tom Artoise; UJ, Ulf Jondelius; YJ, Yilva Jondelius.

Station	Date	Locality	Habitat description	Depth (m)	Collectors	Metabarcoding sample	Latitude	Longitude
1	14.7.19	Praia do Fogo	subtidal (snorkeling), medium coarse sand	3.0-4.0	TA, UJ, YJ		37,7305	-25,311092
2	14.7.19	Praia do Fogo	subtidal (snorkeling), medium coarse sand, water line sediment	4.0-5.0	TA, UJ, YJ		37,7305	-25,311092
3	14.7.19	Praia do Fogo	beach sediment (digging), medium coarse sand, flat area top surface 30 cm	0.0	TA, UJ, YJ		37,7305	-25,311092
4	14.7.19	Praia dos Moínhos	fresh water outlet, beach sediment (digging), fine sand	0.3	TA, UJ, YJ		37,824582	-25,447128
5	14.7.19	Praia dos Moínhos	subtidal (snorkeling), sand between rocks, fine sand	3.0-5.0	TA, UJ, YJ		37,824582	-25,447128
6	14.7.19	Praia dos Moínhos	subtidal (snorkeling), sand collected off of algae/ organic material, fine sand	4.0	TA, UJ, YJ		37,824582	-25,447128
7	14.7.19	Marina	mud (sediment grab), harbour of marina wall	7.0	AMG, FG, FSB, LT, MD, NL		37,7408429	-25,658396
8	15.7.19	Praia das Milícias (Populo)	beach sediment (digging), fine sand	0.0	AMG, FG, FSB, LT, MD, NL		37,750533	-25,623467*
9	15.7.19	Praia das Milícias (Populo)	subtidal (snorkeling), fine sand	2.5	AMG, FG, FSB, LT, MD, NL	y	37,7494	-25,623398
9b	15.7.19	Praia das Milícias (Populo)	subtidal (snorkeling), fine sand	2.5	AMG, FG, FSB, LT, MD, NL		37,7494	-25,623398
10	15.7.19	Praia das Milícias (Populo)	intertidal sediment of the water line, fine sand	0.0	AMG, FG, FSB, LT, MD, NL		37,750533	-25,623467*
11	15.7.19	Praia das Milícias (Populo)	low intertidal, beach dropout, fine sand	0.5	AMG, FG, FSB, LT, MD, NL		37,750533	-25,623467
12	15.7.19	Ilhéu de Rosto de Cão	low intertidal, fine sand	1.3-3.0	UJ, YJ		37,744306	-25,638563
13	15.7.19	Ilhéu de Rosto de Cão	low intertidal, fine sand	1.0	UJ, YJ		37,744306	-25,638563
14	15.7.19	Ilhéu de Rosto de Cão	algae	3.0-3.5	UJ, YJ		37,744306	-25,638563
15a	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	17.7	AZB, FG, KMJ, NDS		37,74	-25,57495*
15b	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	17.7	AZB, FG, KMJ, NDS	y	37,74	-25,57495*
15c	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	17.7	AZB, FG, KMJ, NDS		37,74	-25,57495*
16a	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	18.0	AZB, FG, KMJ, NDS		37,74	-25,57495*
17	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	17.0	AZB, FG, KMJ, NDS		37,74	-25,57495*
18			no station					
19	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	18.0	AZB, FG, KMJ, NDS		37,74	-25,57495*
20	16.7.19	Piscinas Lagoa	subtidal (SCUBA), large sand plains with interspersed rocks, sand with ripple ridges from waves, medium coarse sand	18.0	AZB, FG, KMJ, NDS		37,74	-25,57495*
21	16.7.19	Ilhéu de Rosto de Cão	intertidal (low tide), sand patches between rocks, lots of algae, medium coarse sand	0.0	AP, FSB, JN, MD, NDS		37,7441	-25,6384
22	16.7.19	Praia das Milícias	intertidal (low tide), from water line, swash zone, medium coarse sand	0.0	AP, FSB, JN, MD, NDS	y	37,750444	-25,623372
23	16.7.19	Praia das Milícias	shallow subtidal (low tide) off the beach, medium coarse sand	1.0	AP, FSB, JN, MD, NDS		37,750268	-25,6235
24	16.7.19	Praia das Milícias	subtidal (snorkeling), medium coarse sand	3.0-4.0	AP, FSB, JN, MD, NDS		37,7494	-25,623398
25	16.7.19	Praia de Mosteiros	shallow subtidal, in rock pools on rocky beach, gravel	1.0	MCC		37,889	-25,825
26a	16.7.19	Porto de Mosteiros	subtidal (snorkeling), off rocky beach, gravel	2.0	FSB		37,893701	-25,822045
26b	17.7.19	Porto de Mosteiros	shallow subtidal, off rocky beach, gravel	1.0	MCC		37,893701	-25,822045
27a	17.7.19	Ponta dos Mosteiros	shallow subtidal, in rock pools on rocky beach, gravel	0.2	TN		37,900667	-25,817803
27b	17.7.19	Ponta dos Mosteiros	shallow subtidal, in rock pools on rocky beach, gravel	0.2	MCC	y	37,900667	-25,817803

Station	Date	Locality	Habitat description	Depth (m)	Collectors	Metabarcoding sample	Latitude	Longitude
28a	18.7.19	Lombo Gordo	intertidal, from water line, swash zone, fine sand	0.0	NDS	y	37,785571	-25,141696
28b	18.7.19	Lombo Gordo	intertidal, from water line, swash zone, fine sand	0.0	AP		37,785571	-25,141696
29a	18.7.19	Lombo Gordo	subtidal (snorkeling), sand with ripples from waves	2.0-3.0	NL		37,7857	-25,1413
29b	18.7.19	Lombo Gordo	subtidal (snorkeling), sand with ripples from waves	2.0-3.0	FG		37,7857	-25,1413
30	18.7.19	Lombo Gordo	subtidal (snorkeling), sand with ripples from waves	2.0-2.5	NL		37,7857	-25,1413
31	18.7.19	Lombo Gordo	intertidal, from water line, sand among rocks, swash zone, fine sand	0.0	FG, NL	y	37,786883	-25,14234
32	18.7.19	Santa Barbara	intertidal, sand among large rocks, fine sand	0.0	FG, NDS		37,8197	-25,5413
33	18.7.19	Santa Barbara	intertidal, low end of swash zone, medium coarse sand	0.0	AP, NL		37,8197	-25,5418
34	19.7.19	Capelas	subtidal (SCUBA), sand deposited between rocks, medium coarse sand	11.6	FG, KMJ	y	37,843297	-25,687201
35	19.7.19	Capelas	subtidal (SCUBA), sand plain, sand off ripples, medium coarse sand	14.6	FG, KMJ		37,843672	-25,687457
36	19.7.19	Capelas	subtidal (SCUBA), sand plain, seaward side of large boulders, medium coarse sand	16.0	FG, KMJ	y	37,843863	-25,687351
37	19.7.19	Capelas	subtidal (SCUBA), sand plain, sand of ripples covered with floating brown and green algae, medium coarse sand	14.6	FG, KMJ		37,843672	-25,687457
38	19.7.19	Capelas	subtidal (SCUBA), sand patches between rocks, sand off ripples, medium coarse sand	10.6	FG, KMJ		37,843297	-25,687201
39	19.7.19	Capelas	subtidal (snorkeling), sand patches between rocks along the bay, medium coarse sand	3.0	NDS		37,842201	-25,687555
40	19.7.19	Capelas	subtidal (snorkeling), sand patches between rocks along the bay, medium coarse sand	2.0	NDS		37,842366	-25,687178
41	19.7.19	Capelas	subtidal (snorkeling), sand patches between rocks along the bay, medium coarse sand	2.0	AZB		37,842366	-25,687178
42	19.7.19	Capelas	subtidal (snorkeling), sand patches between rocks along the bay, medium coarse sand	2.0	IC		37,841776	-25,688762
43	20.7.19	Maia	low intertidal, sand patches between rocks and algae, medium coarse sand	0.5	JFP		37,8341	-25,3863
44a	20.7.19	Maia	subtidal (snorkeling), small sand patches on rocky bottom	5.0	MCG		37,8342	-25,3885
44b	20.7.19	Maia	subtidal (snorkeling), small sand patches on rocky bottom	2.0	YI, FSB		37,833921	-25,388654
45	20.7.19	Praia dos Moínhos	subtidal (snorkeling), small sand patches on rocky bottom	2.0	MCG		37,8245	-25,4457
46	20.7.19	Praia dos Moínhos	subtidal (snorkeling), small sand patches on rocky bottom	3.0	YI, FSB		37,8242	-25,445744
47	20.7.19	Praia dos Moínhos	subtidal (snorkeling), small sand patches on rocky bottom	2.0	MCG	y	37,8245	-25,4457
48	20.7.19	Praia dos Moínhos	subtidal (snorkeling), large sand patches interspersed by rocks	2.0	MCG		37,8245	-25,4457
49	22.7.19	Ribérinha	subtidal (snorkeling), large sand patches interspersed by rocks	4.0	YI, FSB		37,82489	-25,446873
50	22.7.19	Ribérinha	subtidal (SCUBA), holdierfield on sandy bottom, deposits of coarse sand	3.0	FG, KMJ		37,836074	-25,484111
51	22.7.19	Ribérinha	subtidal (SCUBA), holdierfield on sandy bottom, deposits of coarse sand	8.5	FG, KMJ		37,836171	-25,483941
52	22.7.19	Ribérinha	subtidal (SCUBA), holdierfield on sandy bottom, deposits of coarse sand	8.8	FG, KMJ		37,83636	-25,483757
53	22.7.19	Ribérinha	subtidal (SCUBA), holdierfield on sandy bottom, deposits of coarse sand	9.4	FG, KMJ		37,836494	-25,483536
54	22.7.19	Ribérinha	subtidal (SCUBA), open sand plain near islet, medium coarse sand	16.2	FG, KMJ	y	37,835631	-25,482362
55	23.7.19	Ribérinha	subtidal (SCUBA), large sand patches between boulders, medium coarse sand	4.6	FG, KMJ	y	37,835755	-25,483437
F1	20.7.19	Lagoa do Peixe	medium coarse sand		AM, AMG	y	37,750533	-25,624647
F2	20.7.19	Sete Cidades - Lagoa Azul from bridge	small freshwater lake with <i>Potamogeton peltogifolius</i> , plankton sample (3 draws)	0	DF		37,81873	-25,73651*
F3	20.7.19	Sete Cidades - Lagoa Azul, lichen from wall	large, shallow freshwater lake, plankton sample (net tossed from the bridge, 3 draws)	0	DF		37,85636	-25,78661*
F4	20.7.19	Sete Cidades - Lagoa Verde	lichen scraped from rocky wall, terrestrial lichen sample	0	DF		37,855382	-25,786896
F5	20.7.19	Sete Cidades - Lagoa Azul next to tunnel	shallow freshwater lake rich in aquatic vegetation, sample of mix of aquatic plants	0.0-0.1	DF		37,854674	-25,78867
F6	20.7.19	Sete Cidades - tunnel entrance	large, shallow freshwater lake, plankton sample from deeper part of the lake (3 draws)	0	DF		37,875266	-25,789561
F7	20.7.19	Sete Cidades - near tunnel	liverwort growing at the entrance of the tunnel, terrestrial liverwort sample	0	DF		37,87604	-25,791098
F8	23.7.19	Graminhais	<i>Selaginella kraussiana</i> clubmoss growing in the shady area near the tunnel entrance, terrestrial clubmoss sample	0	DF		37,875639	-25,790465
			<i>Sphagnum</i> moss, <i>Sphagnum</i> bog 943 m elevation, terrestrial moss sample	0.1	DF		37,80071	-25,2394

TABLE 2. Granulometry across the major sites (see Figure 1) sampled during Meiozoers2019 as retrieved from classified image analyses (see also Figure 2), providing the relative percentage of the different grain size classes.

Major sites_stations	pebble	granules	very coarse sand	coarse sand	medium sand	fine sand	very fine sand	coarse silt
Praia do Fogo_St1	0.000	0.031	0.508	5.617	50.554	41.782	1.370	0.139
Marina_St7	0.016	0.048	0.238	2.584	10.005	69.938	17.156	0.016
Praia das Milícias_st11	0.000	0.070	1.643	14.930	63.601	18.566	1.189	0.000
Sao Roco_St12	0.000	0.000	0.077	5.600	42.755	39.410	10.760	1.397
Piscinas Lagoa_St15b	0.000	0.214	3.419	15.079	26.526	28.144	20.788	5.830
Ilhéu de São Roque_St21	0.038	0.189	0.490	12.733	41.275	43.935	1.339	0.000
Praia das Milícias_St24	0.000	0.000	0.199	7.824	50.565	40.480	0.932	0.000
Praia de Mosteiros_St25	1.780	6.754	21.355	47.280	9.585	10.718	2.224	0.020
Praia de Mosteiros_St26	0.423	4.495	34.638	44.104	6.980	7.985	1.322	0.000
Praia de Mosteiros_St27	0.842	7.628	24.988	29.153	14.460	16.846	5.756	0.140
Lombo Gordo_St28	0.000	0.000	0.385	14.722	65.416	14.116	3.975	1.387
Santa Barbara_St32	0.000	0.286	5.685	56.319	28.221	8.507	0.982	0.000
Santa Barbara_St33	0.000	1.716	9.438	47.378	33.174	6.768	1.430	0.095
Capelas_St34	0.000	0.140	6.130	23.959	47.309	21.151	1.263	0.047
Maia_St43	0.000	1.100	18.775	43.598	13.747	17.439	5.263	0.079
Praia dos Moinhos_St46	0.000	0.000	8.190	46.163	19.874	10.882	11.856	3.036
Riberinha_St51	0.260	3.115	11.616	16.223	12.524	13.368	22.972	19.792
Riberinha_St53	0.000	0.033	0.300	5.047	40.169	38.166	12.514	3.771

morphological data (molecular data still pending, see Norenburg *et al.*, 2021) in the genera *Ototyphlonemertes* spp. and *Cephalothrix* spp. (the latter traditionally not classified as meiofauna).

Moreover, we collected one species (39 specimens) of the rare interstitial cnidarian *Halanmohydra*, which morphologically presents a mix of character between NE Atlantic *H. schulzei* and *H. intermedia*, preliminary assigned to *H. schulzei* awaiting molecular confirmation (see Tödter & Schmidt-Rhaesa, 2021).

In the marine habitat, we recorded 3 species of Rotifera, *Synchaeta neapolitana* and two potentially new to science: *Rotaria* sp. and *Testudinella* sp. In freshwater habitats at least 20 species were present, however likely none new to science (see Fontaneto *et al.*, 2021).

We have not discovered any kinorhynchs among sediments samples (one species of *Echinoderes* sp. was discovered in algae samples, however), nor any tardigrades, nor Loricifera, but sampling strategy and site selection might have been inadequate for their discovery.

Characteristic meiofauna of the São Miguel coastal sediments

In general, the occurrence of meiofauna is highly patchy and recollection can be a matter of luck and patience. Most of the herein recorded Azorean meiofauna diversity relates to single findings or only relies on few specimens collected at a single station. Only a few taxa were common or even abundant at certain stations or across specific habitats in São Miguel shallow-water sediments during the Meiozoores2019 workshop.

Among nematodes, the genera *Euchromadora*, *Theristus* and *Symplocostoma*, *Desmodora* (see Figure 3E-F for examples) were common and found on several subtidal stations. The annelids *Lindrilus* sp. and *Claudrilus* cf. *hypoleucus* (Protodrilidae)

were common at intertidal sites with gravel and very coarse sand, while *Microphthalmus* cf. *pseudoaberrans* (Microphthalmidae) and *Mesonerilla* cf. *luederitzi* (Nerillidae, Figure 3C) were common in subtidal samples of medium-coarse sands (Martínez *et al.* 2021). Among gastrotrichs, specimens of the genera *Paraturbanella* and *Tetranchyroderma* occurred at three or more stations (see Araújo & Hochberg, 2021). The proseriate *Otoplana* cf. *bosporana* (Figure 3A) was abundant in the intertidal surf zone, *Paratoplana* and *Duplominona* spp. (Figure 3B for an example) were abundant in several subtidal stations (Curini-Galletti, 2021). Among rhabdocoels only *Ancistrorhynchus ischnurus* L’Hardy, 1963 occurred at more than three stations. Among molluscs, only

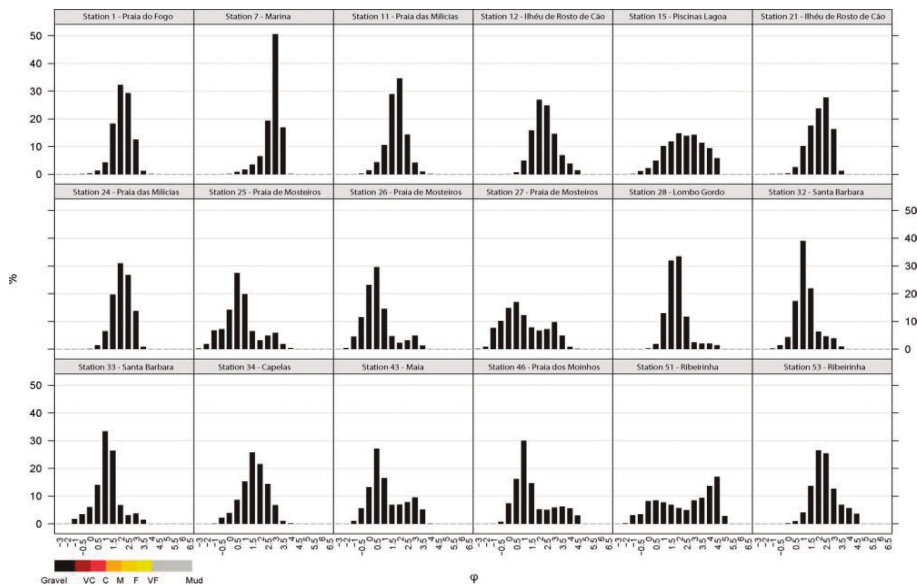


FIGURE 2. Distribution of grain size at selected stations representing all major sites sampled during Meiozoores2019. Granulometry retrieved from classified image analyses (see also Table 2).), c, coarse sand; f, fine sand; m, medium sand; vc, very coarse sand; vf, very fine sand.

pholidoskepid solenogastres *Dondersia todtae* Klink, Bergmeier, Neusser & Jörgen, 2015 (Figure 3D) was collected in reasonable numbers and was encountered at five different stations (see Neusser *et al.* 2021).

DISCUSSION

Meiofaunal diversity of the Azores

The present study revealed a moderate species diversity of soft-bodied meiofauna in the intertidal and shallow subtidal sediments of São Miguel Island with approx. 180 recorded species. This is in apparent contrast to the depauperate macrofauna of marine sediments – concerning both species diversity, as well as abundance and biomass – previously discussed to result from the instability of marine sediments of the high-energy coast of the Azores (Bamber & Robbins, 2009). We found several locally abundant meiofaunal species (see Figure 3 for examples), which colonized Azorean sediments and successfully cope with the local conditions.

Direct comparison of numbers from species inventories in meiofauna as a proxy for diversity estimates is problematic, not only for the evident focus on partially different taxa, but also due to inconsistent overall sampling effort, independent sampling strategies related to the specific local sediments and available taxonomic knowledge and expertise prior to the initiatives. Nevertheless, some general trends comparing data on meiofaunal diversity from the North-East Atlantic continental sediments and oceanic islands are worth discussing:

The species diversity of five main groups of meiofauna (Acoelomorpha, Proseriata, Rhabdozoa, Gastrotricha and

Annelida) was considerably higher (up to a maximum of three-folds) in similar sampling campaigns along the European continental coast of Sweden (Willems *et al.*, 2009) and Mediterranean Sardinia (Curini-Galletti *et al.*, 2012) (see Table 4 for a comparison of species numbers). Evidently, there is a strong taxonomic bias towards the comparably well-known and explored meiofauna from the European coastline, given the long history of meiofauna research at several marine research stations (*e.g.*, Swedmark, 1964; Ax, 1969; Coull & Giere, 1988), providing taxonomic keys for identification as well as knowledge on localities, habitat preferences and even seasonal effects. But in particular, the high numbers of still undescribed species discovered during the Swedish and Italian meiofauna surveys demonstrate that the continental European meiofauna is still far from being completely surveyed and shows that species diversity is likely truly considerably higher on the continental coasts of the North-East Atlantic and especially the Western Mediterranean (approx. 37% of 203 species are considered new to science (Curini-Galletti *et al.*, 2012) – compared to only approx. 15% recorded herein).

Available comparative data from other isolated archipelagos shows throughout lower levels of species diversity than continental sampling events, with the unique exception of the Canary Islands (see Table 4 for a summary). Summarizing a large biodiversity exploration to the Galapagos Islands, (Westheide, 1991) for example reports approx. 390 species of meiofauna from the Galapagos, however, also including species-rich arthropod taxa such as harpacticoid copepods, ostracods

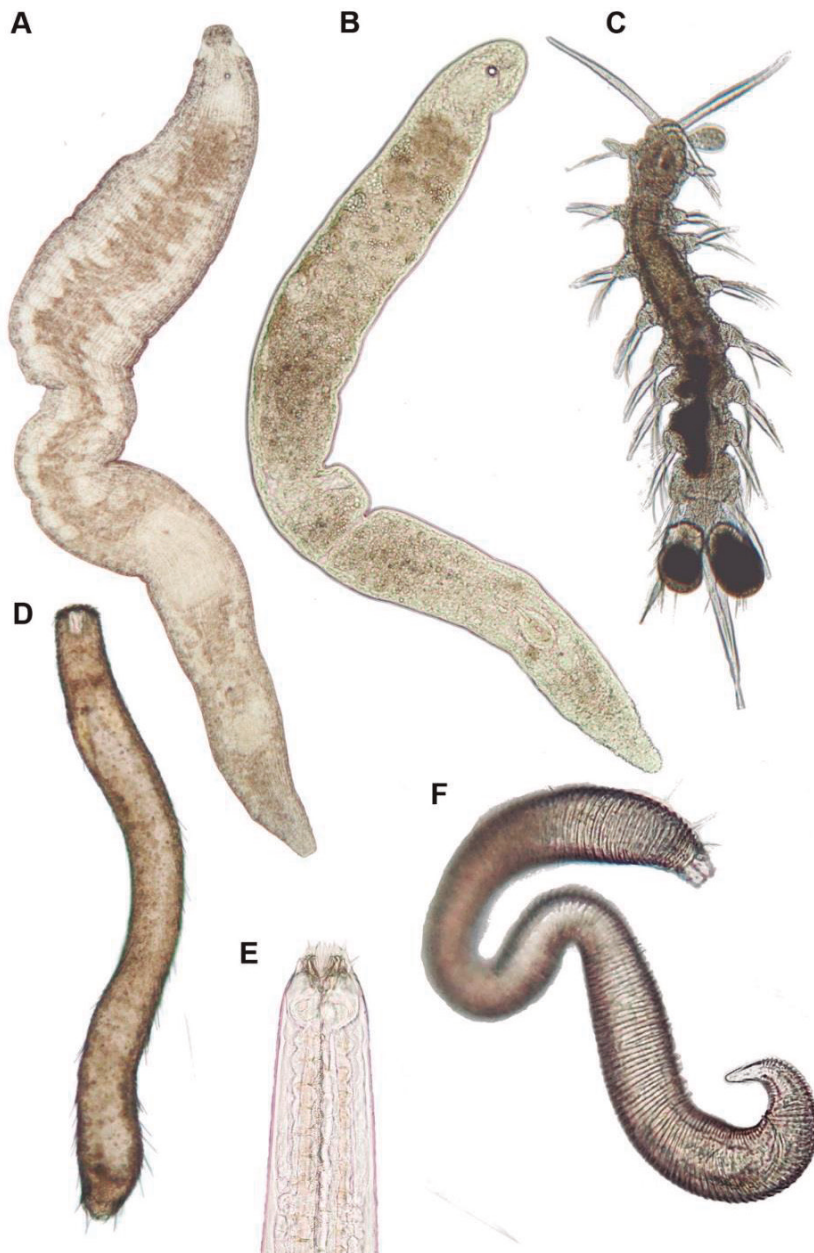


FIGURE 3. Common meiofauna of the Azores (not to scale). **A-B**, Proseriate platyhelminthes: **A**, *Otoplana cf. bosporana* (approx. 1.5 mm); **B**, *Duplominona* sp. (approx. 1 mm). **C**, Polychaete annelid *Mesonerilla cf. luederitzi* (approx. 0.5 mm). **D**, Solenogaster molluscs *Dondersia todtae* (approx. 1 mm). **E-F**, Nematoda: **E**, Thoracostomopsidae; **F**, Epsilonematidae (approx. 0.8 mm).

and halacarid acari. Comparing the taxa in focus, *e.g.*, selected families of interstitial annelid species (see Martínez *et al.*, 2021), Nermerteia, Acoelomorpha, Gastrotricha or proseriate Platyhelminthes species-level diversity is similar or slightly lower than the one recorded herein for the Azores (Table 4). In contrast, data from a smaller scale meiofauna workshop held on the Hawai'i archipelago in the Pacific (see Table 4, own unpublished data) recorded higher species diversity especially concerning molluscs and

nemerteans, whose paucity in Azorean sediments was surprising. Uniquely, among oceanic islands a large meiofauna workshop of Lanzarote Island yielded a significantly higher species list, in particular related to interstitial families of polychaete annelids, gastrotrichs and proseriate flatworms (Table 4). This high level of diversity cannot entirely be explained by the more intense sampling effort during the workshop (Martínez *et al.*, 2019), but is likely also attributed to the different geographical and

TABLE 3. Diversity of Acoelomorpha collected during Meiozozos2019. Updates to the taxonomic ID as well as photos and other specimen data are available through the acoelomorph-database (<http://acoela.myspecies.info/en/taxonmap>).

Tentative taxonomic ID	Locality name	Sample ID	specimen ID	Previously recorded from NE Atlantic	Previously recorded from Mediterranean
Acoela					
Convolvutidae					
<i>Convolvuta convoluta</i>	Piscinas Lagoa	Sample AZ 17	19-261	Yes	Yes
Dakuidae					
<i>Philactinoposthia sp-30</i>	Praia dos Moinhos	Sample AZ 46	19-275	-	-
Diopisthoporidae					
<i>Diopisthoporus sp-1</i>	Riberinha	sample AZ53	19-281, 19-286 -293	-	-
Isodiametridae					
<i>Atogina marci</i>	Ilheu São Roque	Sample AZ 21	19-252, 19-257	Yes	Yes
<i>Praeaphanostoma sp-3</i>	Riberinha	sample AZ49, AZ50	19-277-19-279, 19-284, 19-285	-	-
<i>Proconvoluta primitiva</i>	Ilheu São Roque, Praia dos Moinhos, Riberinha	Sample AZ16, 21, 46,53	19-258, 19-260, 19-276, 19-283	Yes	No
Mecynostomidae					
<i>Eumecynostomum sp-5</i>	Piscinas Lagoa	Sample AZ 17	19-259	Yes	Yes
<i>Mecynostomum sp-6</i>	Capelas	Sample AZ 36	19-268-269	Yes	No
<i>Mecynostomum sp-19</i>	Capelas	Sample AZ 36	19-270-271	-	-
<i>Paramecynostomum diversicolor</i>	Ponta Delgada harbour	algae	19-264, 19-265	Yes	Yes
Proporidae					
<i>Kuma sp-5</i>	Piscinas Lagoa	Sample AZ 15	19-251, 19-253-256	Yes	Yes
<i>Parahaploposthia sp-2</i>	Piscinas Lagoa	Sample AZ 16	19-262	-	-
Nemertodermatida					
Ascopariidae					
<i>Flagelophora apelti</i>	Piscinas Lagoa	Sample AZ 16	19-263	Yes	Yes
Nemertodermatidae					
<i>Sterreria sp.</i>	Capelas, Riberinha	Sample AZ 34, 36, 37, 53, 54	19-267, 19-272-19-274, 19-280, 19-282	Yes	Yes

geological features of the different oceanic archipelagos:

Geographic isolation - Lower species diversity on oceanic islands meets the general expectations on diversity patterns of meiofauna, which are usually considered as poor dispersers: due to their minute body sizes the active dispersal range via locomotion is particularly low and most groups lack planktonic larvae, which allow for long-distance dispersal to reach oceanic islands (Gerlach, 1977; Palmer, 1988). Thus, amphioceanic or even cosmopolitan distribution ranges have been coined as 'meiofauna paradox' and in search of an explanation numerous studies have investigated the different means of passive dispersal of marine meiofaunal organisms: 1) via drifting in the water column after suspension by wave shoaling or tidal currents (e.g., Palmer, 1988); 2) via rafting either on biogenic items (such as algae, driftwood or marine snow) or on abiotic items (such as plastic or volcanic pumice) (e.g., Jokiel, 1990); 3) via zoochory, with turtles likely serving as one of the most important epizoochoric vectors for meiofauna in the marine environment (Ingels *et al.*, 2020); or 4) via anthropogenic vectors, e.g., through the ballast water of ships (e.g. Gerlach, 1977). At least drafting and rafting highly depend on sea-surface currents and winds, which need to be analyzed in a historic context. While there is direct evidence for these different means of long-distance dispersal in certain meiofaunal taxa (particularly well studied on Nematoda, see Ptatscheck & Traunspurger (2020) for a recent review), the predominant means of passive dispersal remain speculative

for many groups, which exhibit wide distribution ranges and are recorded from oceanic islands. Distribution ranges seem to highly depend on taxon specific attributes, which allow for one of the aforementioned passive dispersal mechanisms. In fact, many cases of cosmopolitanism across major groups of meiofauna collapse in the light of molecular data, which frequently reveal a high degree of cryptic speciation misleading taxonomy and subsequent biogeographic hypotheses on broad distribution ranges (e.g., Westheide & Schmidt, 2003; Jörger *et al.*, 2012; Leasi & Norenburg, 2014; Meyer-Wachsmuth *et al.*, 2014; Scarpa *et al.*, 2016; Cerca *et al.*, 2018). This contrasts the "everything is everywhere" or ubiquity hypothesis (Fenchel & Finlay, 2004) arguing that microscopic organisms usually show cosmopolitan distribution ranges and consequently no clear biogeographic patterns or areas of endemism. Even though this is clearly an overstatement and certain geographic patterns are visible also in microscopic animals such as rotifers, it still holds true, that wide distribution ranges do exist (Fontaneto *et al.*, 2008). The ability for passive long-distance dispersal highly depends on dormancy abilities, long-term resistance of dormant stages and the ability to colonize and reproduce quickly in new places (Fontaneto, 2019). Dormant propagules (e.g., resting eggs) are prominent in terrestrial and fresh-water nematodes, tardigrades and rotifers, whose ability to survive extreme desiccation also allows for airborne dispersal and phoresy via sea birds (see Fontaneto, 2019 for review), but also accounts responsible for variable species-specific long-distance dispersal abilities in marine species of these meiofaunal groups (e.g., Artois *et*

al., 2011; Ptatscheck & Traunspurger, 2020). Molecular evidence for an exceptionally broad, boreal distribution range of an interstitial annelid – *Dinophilus vorticoides* Schmidt, 1848 – with dormant encystment stages suggests that also in other marine meiofauna groups dormancy might play a significant, still underestimated role in long-distance dispersal (Worsaae *et al.*, 2019).

Suitable sediments – Next to taxon-specific traits that enable long-distance dispersal, the chance that “survivors” arriving on oceanic islands are able to colonize the new place

successfully relates to the suitability of the encountered habitats, the taxon-specific ability to cope and adapt to different biotic and abiotic environmental conditions and to the species-specific traits in reproduction to establish a population: most sediments sampled (so far) on São Miguel, Azores were poorly sorted, i.e. contained a considerable portion of fine, silty particles (see Figure 2) and were dominated by basalt and volcanic ashes. While the Azorean nematofauna seems to be able to cope with different sediment properties (the encountered genera are usually found in muddy

TABLE 4. Comparison of the species diversity found during Meiozores2019 with results of other meiofaunal sampling campaigns in the North-East Atlantic and Mediterranean and on other oceanic islands. Galapagos islands in 1972-73 (Westheide, 1991); Tjörnö, Western Sweden 2007 (Willems *et al.*, 2009); Northern Sardinia in 2010 (Curini-Galletti *et al.*, 2012); Lanzarote, Canary Islands 2011 (Martínez *et al.*, 2019); Hawai’i 2017 (own unpublished data). († JLN pers. observation; “-”, no data available from the respective workshop; *, limited to entirely interstitial families; **, sampling event not targeted to interstitial annelids; ***, restricted to the genus Othothyphlonemertes, excluding Cephalothrix due to a lack of comparative data).

Taxon	# of species found during the workshop	# of undescribed species	# of species with uncertain status
Northeastern Atlantic and Mediterranean (Azores/ Canary Islands/ Sweden/ Sardinia)			
Acoelomorpha	14 / - / 27 / 28	5 / - / 8 / 21	0 / - / 0 / 4
Proseriata	24 / 39 / 21 / 34	10 / 33 / 3 / 18	4 / 4 / 0 / 1
Rhabdocoela	29 / 74 / 35 / 55	13 / 29 / 3 / 21	9 / 36 / 1 / 13
Gastrotricha	21 / 61 / 43 / 60	4 / 8 / 11 / 17	7 / 19 / 0 / 6
Annelida	12 / 36 / 6** / 16	3 / 11 / 0 / 0	6 / 6 / 0 / 5
Nemertea***	3 / 6 / 1 / 2	1 / 2 / 0 / 0	0 / 1 / 0 / 0
Oceanic islands (Azores/ Canary Islands/ Galapagos/ Hawai’i)			
Acoelomorpha	14 / - / 16 / ?	5 / - / 15 / ?	0 / - / 1 / ?
Proseriata	24 / 39 / 17 / 25	10 / 33 / 16 / 14	0 / 4 / 0 / 0
Rhabdocoela	29 / 74 / 29 / ?	13 / 29 / 28 / ?	0 / 36 / 0 / ?
Gastrotricha	21 / 61 / 23 / -	9 / 8 / 18 / -	7 / 19 / 5 / -
Annelida*	12 / 36 / 13 / 18	3 / 11 / 10 / 12	6 / 6 / 2 / 2
Mollusca	9 / 4 / - / 22	5 / 3 / - / 18	1 / 0 / - / 4
Nemertea***	3 / 6 / 7 / 3	1 / 1 / 2 / 8	0 / 1 / 0 / 0

sediments rich in organic matter in other parts of the world – AJN and VA, own observations), other taxa – such as Nemertea and Mollusca – exhibit a preference towards coarse clean sands and shell hash, which might explain their paucity on the Azores when compared to other oceanic islands like *e.g.*, the Hawai'i archipelago (see Table 4). Investigating the influence on species composition on Lanzarote, Canary Islands the differences of habitats (*i.e.*, ponds, caves, subtidal and sandy beaches) unsurprisingly had the greatest effect (Martínez *et al.*, 2019) and current diversity data on Azorean meiofauna is likely largely influenced by the uniformity of subtidal and intertidal habitats investigated so far on São Miguel.

Island ontogeny – The relative closeness to the shore and the presence and diversity of suitable substrates likely account for the comparable high meiofaunal species diversity on the Canary Islands (Martínez *et al.*, 2019). But evidently, distance from the nearest continent and the availability of suitable substrates are not the only major factors influencing the marine meiofaunal diversity on oceanic islands. Understanding current diversity patterns of marine species on oceanic island requires a historic perspective on island dynamics, *i.e.* on their age setting the timeframe for arrival, colonization and speciation (with the Azores being particularly young with only 0.7-6 my (Ramalho *et al.*, 2017)), on their (submarine) topography and extent of their shelf area, as well as on the presence of submerged banks as seamounts serving as stepping stone in dispersal of meiofaunal organisms (George, 2013). The sediment infauna and likely also the interstitial meiofauna

of reef-less oceanic islands like the Azores is highly affected by drops in sea level during glacial periods, which can be accompanied with a disappearance of sediment substrates, especially if the sea level falls below the shelf break (Ávila *et al.*, 2008). The comparably steeper island slopes and shallower shelf break compared to continental coasts can lead to the effect that winter storms transport sediments offshore and permanently disappear (Quartau *et al.*, 2012; Ávila *et al.*, 2019), with catastrophic consequences for the associated meiofauna. Next to the favorable availability of coarse calcareous sediments, the higher diversity levels in meiofauna recorded from Hawai'i (see Table 4) in comparison to the Azores might also be influenced by the extensive areas of reef habitats, atolls, submerged banks and seamounts and a gradual slope to the shelf break at around 100 to 200 m (Meyer *et al.*, 2018) making it less vulnerable to severe sediment loss during eustatic sea-level changes.

Evaluating the rate of endemism and the taxonomic misfortune of missing primary data

Out of the 8047 species known from the Azorean fauna and flora, 411 are considered as endemic (Borges *et al.*, 2010), accounting for approx. 5% of the local biodiversity. Most of the Azorean endemics are terrestrial arthropods and snails (Borges *et al.*, 2010; Martins, 2011), while the evidence for endemism in the Azorean marine biota is sparse (*e.g.*, Morton & Britton, 2000a; Morton & Britton, 2000b), with only single examples among coastal fish, arthropods and few more among microgastropods (*e.g.*, Rissoidea (Gofas, 1990) or Ellobiidae (Martins, 1995)), which

might have arrived rafting on algae to the islands. However, this putative low rate of endemism in the marine biota might suffer from a taxonomic inaccuracy, as several groups of marine invertebrates have not been sampled in depth and reanalyzes of historic records assigned to known European species with modern methods might reveal delineating morphological differences to the well-known European sibling species (see *e.g.* Micael *et al.*, 2019 on Bryozoa).

A modelling study to identify areas of endemism using parsimony based on a global inventory of meiobenthic annelids, tardigrades, gastrotrichs, and kinorhynchs accounting for geographical sampling bias reconstructed similar areas to those from comparative studies on macrofaunal marine invertebrates (Costello *et al.*, 2017), but suggesting smaller spatial units for ecological and biogeographic areas (Garraffoni *et al.*, 2021). Their parsimony analysis of endemism identified the Azores as area of endemism within the maximum range extension of the North-East Atlantic area of endemism, extending along the European Coast line (including the Canary Islands) (Garraffoni *et al.*, 2021), a concept challenged, however, by other studies on biogeographic entities and shared endemism among North-East Atlantic Macaronesian archipelagos (Spalding *et al.*, 2007; Freitas *et al.*, 2019; see discussion below).

By default, all meiofauna species discovered in the present study, which are new to science (approx. 15% of the recorded species), are at the current state of knowledge endemic species to the Azores. Thus, the only yet formally described endemic

meiofauna species – the gastrotrich *Crasiella azorensis* Hummon, 2008 (recorded previously from Faial and now also from São Miguel) (Hummon, 2008; Araújo & Hochberg, 2021) – will likely be accompanied in the future by a series of meiofaunal taxa unique in the Azorean fauna. But unfortunately, the meiofauna across the North-East Atlantic Macaronesian archipelagos is still poorly explored, and it thus remains unclear whether these putative endemics are truly exclusive faunal components of the Azores or just result from a current taxonomic bias due to a lack of primary species data from neighboring provinces, which might share (yet undiscovered) populations.

While further sampling on the other North-East Atlantic islands might reveal broader distribution ranges of the encountered Azorean meiofauna species, resulting in shared endemics for certain archipelagos, further analyses of the collected material might augment the rate of endemic species: in the present study, we have not discovered any morphological apparent clusters of closely related species of the meiofauna taxa in focus, which could be interpreted as local radiations of successors from early immigrants adapting to novel ecological niches in the new surroundings. ‘Darwin finch’-like radiations might either be truly absent from our initial inventory or still hidden among morphological highly static taxa. Meiofauna is especially prone to cryptic speciation, due to the highly adapted bauplans to the mesopsammic environment, requiring molecular data for species delimitation (*e.g.*, Jörger *et al.*, 2012; Leasi & Norenburg, 2014; Meyer-Wachsmuth *et al.*, 2014; Cerca *et al.*,

2020).

Generally, we assume that species-specific dispersal abilities negatively correlate with the rate of endemism, i.e. that the presence of pelagic dispersal stages or dormant stages allow for wider distribution ranges (Curini-Galletti *et al.*, 2012). But analyses of the Lanzarote meiofauna revealed no correlation between body size and dispersal with the percentage of endemic species encountered on the Canary Islands (Martínez *et al.*, 2019). Only reproduction, i.e. the proportion of parthenogenetic species, was negatively correlated to the number of endemic species (Martínez *et al.*, 2019). Parthenogenetic species have a better chance to successfully establish a new population from one “chance survivor” arriving to an oceanic island, and geographic isolation can be a driver for subsequent speciation, rendering this result somewhat counterintuitive. This however implies that we view oceanic islands as a sink only, rather than also a source from which gene flow among isolated widely distributed populations is maintained.

Azorean meiofauna – where do you come from?

The incompleteness of species inventories on a global or regional scale clearly affects the biogeographic conclusions and assumptions on spatial distribution patterns – known as the Wallacean shortfall (Hortal *et al.*, 2015) – which is particularly prominent in meiofauna. In the present survey, we found few examples of shared faunal elements between the discovered Azorean meiofauna and elements of the Western Atlantic – most refer to putative amphiatlantic or even cosmopolitan species (e.g. the rhabdocoels *Gyratrix hermaphroditus* Ehrenberg, 1831

(known to be a hyperdiverse complex of semi-cryptic species distributed worldwide) or amphiatlantic *Utelga heinckeii* (Attems, 1897) / *U. pseudoheinckeii* Karling, 1980). Most shared species diversity refers to the North-East Atlantic (see e.g., Table 3 on Acoelomorpha), including species that are also distributed in the Mediterranean. This faunal overlap is in concordance with distribution records of macrofaunal marine species (and also evident in terrestrial biota), which are predominantly of European origin (e.g., Morton & Britton, 2000a; Ávila *et al.*, 2009). Prior to the development of the Gulf Stream in the context with the final closure of the Isthmus of Panama prominent east to westward currents likely facilitated colonization of European species to the Azores, further facilitated by short-lived shallow-water currents during Pleistocene glacial-interglacial cycles (Ávila *et al.*, 2009).

In the present survey, we recorded few shared endemics with the Canary Islands, such as the rhabdocoel *Proschizorhynchus martinezi* Gobert, Reygel & Artois, 2017 or the saccocirrid annelid *Saccocirrus slateri* Di Domenico, Martínez & Worsaae, 2019. Whereas interstitial annelid fauna from São Miguel resembles the one from the Canary Islands, but lower in species richness, the proseriate Platyhelminthes diversity is strikingly different (see Curini-Galletti, 2021). It shows no particular similarities with the fauna documented from the Canary Island and known species from the North-East Atlantic and the Mediterranean, present on the Azores have not yet been recorded from there (Curini-Galletti, 2021). This poor faunal overlap is surprising, as Canary Islands, Madeira, Selvagens, and Azores have been traditionally united as Macaronesia

biogeographic province (partially also including Cabo Verde, which has been controversially debated both based on terrestrial and marine biota) (see Freitas *et al.*, 2019, for a summary). Macaronesia *sensu latu* (including Cabo Verde) was already rejected in the definition of global 'marine ecoregions' by Spalding *et al.* (2007), who defined the temperate North Atlantic as one realm, uniting the Azores, Madeira and the Canary Islands in a single ecoregion - the Lusitania province - while assigning Cabo Verde to the 'Western African transition' in the Tropical Atlantic realm. This exclusion of Cabo Verde from Macaronesia *sensu stricto* was supported by recent analyses of quantitative data from six main marine groups with different dispersal abilities (Freitas *et al.*, 2019). Concerning the Azores their datasets of widely dispersing groups (*e.g.*, macroalgae, coastal fishes, and echinoderms) underpins the inclusion of the archipelago within the remaining Macaronesian islands (*i.e.*, Madeira, Selvagens, and Canary Islands - termed 'Webbnesia'), while the available datasets from other marine taxa (*e.g.*, polychaete annelids, gastropods, and brachiurans) support a separated Azorean ecoregion, which is also supported by a shared endemics analysis (Freitas *et al.*, 2019). The input from meiofauna based on the present survey to the debate of shared vs. separate biogeographic units among the North-East Atlantic Macaronesian archipelagos is unfortunately still limited, and will likely also require a taxa-wide comparative approach to evaluate whether this preliminary impression on a rather poor fauna overlap between the herein reported Azorean meiofauna and the records from Lanzarote (Canary Island) (summarized in Martínez *et al.*, 2019) support the separation of the

Azores from Webbnesia. Intensified and extended meiofauna surveys across the Azorean archipelago and comparative data from other islands of Webbnesia (especially those with virtually unexplored meiofauna such as Madeira or Selvagens) are needed to gather a primary dataset suitable to test biogeographic hypotheses.

OUTLOOK

Never stop exploring: road map to enhance our knowledge on Azorean meiofauna

The present results of the Meiozores2019-workshop hopefully serve as a kick-off for further exploration of the understudied meiofauna of the Azores, which presents a combination of different faunal elements and a wealth of new and potentially endemic species. Future sampling still needs to target additional and still unexplored habitats on São Miguel (*e.g.*, in the deeper subtidal) to complement the present survey on the island's meiofaunal diversity. Future sampling should especially target Ilhéu de Vila Franca due to the likely presence of suitable habitats for several major groups of meiofauna (*i.e.*, coarse well-sorted sediments of biogenic origin/ shell hash, as well as marine caves).

A short sampling trip to Santa Maria directly after the Meiozores2019 workshop by MCG and JN reported suitable coarse sediments and an interesting meiofauna immediately adding further species to our meiofaunal species inventory (see Curini-Galletti, 2021; Neusser *et al.*, 2021). This clearly underlines that the São Miguel meiofauna was just a starting point towards documenting the entire Azorean meiofauna and that more in-depth investigation of the oldest island Santa Maria and

also from the youngest westernmost island is calling for joined sampling trips.

Understanding the evolution and biogeography of Azorean meiofauna requires comparative data from the other North-East Atlantic archipelagos to be able to evaluate rates of endemism and distribution ranges in the different lineages of soft-bodied meiofauna. Especially meiofaunal species inventories from Madeira and Cabo Verde are needed to be able to add the meiofauna perspective to the question of whether Macaronesia (*sensu strictu* or *latu*) forms a coherent biogeographical unit and to evaluate whether the Azores can be considered an area of endemism of its own. This is a joint call for action to provide the taxonomic primary data needed to enhance our understanding of the biogeography of meiofauna in the North Atlantic and enable studies on the effects of taxon-specific traits on distinctiveness in species composition on the different Macaronesian archipelagos.

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