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MEIOLANZA

Patterns of diversity and endemism of soft-bodied meiofauna in an oceanic island, Lanzarote, Canary Islands

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Abstract

Oceanic islands, characterized by high levels of endemism and distinct faunas when compared to neighbouring continents, represent natural evolutionary laboratories for biologists to understand ecological and evolutionary processes. However, most studies on oceanic islands have focused on terrestrial and marine macrofaunal organisms, and ignored microscopic animals. We present here an inventory of all soft-bodied meiofaunal organisms collected during a 2-week workshop on the oceanic island of Lanzarote, Canary Islands. Our checklist included 239 species, with 88 of them endemic to the archipelago. The number of endemic species was lower in groups with a higher proportion of parthenogenetic species, while it was not significantly affected by body size and percentage of species with dispersal stages. A higher percentage of endemic species was found in isolated habitats and environments, with only annelids showing significantly higher number of endemic species in anchialine caves. Our results might be biased by the high number of indeterminate species found in our samples and the lack of knowledge of the meiofauna of the African coast. Our findings, however, provide the first insight of patterns of diversity of soft-bodied meiofauna in Atlantic oceanic islands, suggesting that island endemic species might also exist amongst microscopic animals.

Keywords Anchialine · Annelida · Biogeography · Gastrotricha · Interstitial fauna · Caves · Proseriata · Rhabdocoela · Rotifera

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Introduction

Oceanic islands act as natural evolutionary laboratories for biologists because they are isolated, well delineated areas, comparatively younger and smaller than nearby continental zones, representing unique and independent replicates for evolutionary trajectories (Losos & Ricklefs 2009; Shaw & Gillespie 2016). In contrast to continental islands, oceanic islands have never been in contact with any other landmass, so any organism inhabiting them must have dispersed across oceanic barriers. Studies on macrofaunal biodiversity in oceanic islands usually focus on terrestrial fauna, while the marine fauna has attracted far less attention (Dawson 2016). Whereas terrestrial fauna in oceanic islands typically is characterized by high endemism and differs sharply from its continental counterpart, island marine fauna is less different from the nearby continents, due to the connectivity and dispersal facilitated by ocean currents (Ekman, 1953; Pineda et al. 2007). For example, while the percentage of endemic species in freshwater and terrestrial Hawaiian fauna averages 48%, reaching 95% in some groups, it averages only 11% in the Hawaiian marine fauna (Wagner & Funk 1995; Randall 1998; Paulay & Meyer 2002; Drew & Roderick 2005), though this difference is clouded because the marine fauna (except for fishes) has been less studied. In contrast, the occurrence of marine endemic species in oceanic islands is still significantly higher than what is found in continental marine regions (Meynard et al. 2012; Palacios-Salgado et al. 2012). This suggests that the same processes leading to a higher level of endemic species might affect both terrestrial and oceanic fauna of islands, and that differences between both realms might depend on the ecological and biological traits of different taxa. As a consequence, additional studies comparing a wider range of environmental and biological factors are necessary to understand the ecological and evolutionary processes that favour the origin of endemic species in oceanic islands (Dawson 2016).

The Canary Islands are an oceanic archipelago composed of eight volcanic islands and several islets located on the African Oceanic Plate. The number (ca. 120) and proportion (ca. 2%) of known endemic species in this archipelago's marine habitats is lower than the number (3407) and proportion (36.8%) of endemic species in terrestrial habitats (Moro et al. 2003, Izquierdo et al. 2004). In addition, the number of marine endemic species is not evenly distributed across animal groups. For example, there are only two endemic species amongst the 299 recorded coastal fish (0.7%), which contrasts with the 96 endemic species amongst the 811 species of marine prosobranchs (11.8%) (Ávila et al., 2018). These differences may be related to biological traits found in specific groups, such as the secondary loss of pelagic larvae in several of the gastropod lineages endemic to the island (Curini-Galletti 1985, Moolenbeek and Hoenselaar, 1989, 1998, Gofas 2007), versus the high motility of most species of fish. Yet, no study covered more groups of animals to look for differences and commonalities in the patterns of occurrence of endemic species, in order to provide inference on the potential processes driving endemism. The percentage of endemic species also differs amongst marine habitats, with the most striking case represented by the so-called anchialine ecosystems, hosting a high proportion of endemic species, often limited to one or very few populations (Iliffe et al. 1984). Anchialine habitats consist of land-locked water bodies with marine origin, which are partially isolated from the sea (Stock et al. 1986). Such habitats are relatively common in the Canary Islands, although they mostly consist of open, tidally influenced ponds colonized by marine species (Sangil et al. 2008). Extensive subterranean anchialine ecosystems are only found on the island of Lanzarote (Martínez et al. 2016), favoured by the low precipitation and the porous geological substrate of the island, which allows marine infiltration through the coastline of the island. So far, 38 species out of the 50 recorded species in the anchialine ecosystems of Lanzarote are endemic to the island (Martínez and Gonzalez, 2018). This high proportion of endemic species is probably favoured both by the partial isolation of the anchialine system and by the different ecological conditions that this environment offers compared to the surrounding coastal environments (Martínez et al. 2009).

Most faunistic studies in the coastal habitats of Lanzarote focused on macroscopic organisms, leaving microscopic animals neglected (Moro et al. 2003). This lack of studies not only obscures the contribution of these organisms to local diversity but, given that meiofauna represent a major component of biodiversity (Fonseca et al. 2018), such lack of knowledge might as well affect our understanding of general colonization and diversification processes in the island. We here present an inventory of the majority of soft-bodied meiofauna phyla in the oceanic island of Lanzarote, focusing on different types of aquatic habitats, including anchialine systems. The inventory was produced during the I International Workshop on Anchialine and Marine Meiofauna. This study has a twofold focus. First, we present an updated checklist of the soft-bodied meiofaunal species recorded during the workshop, including a description and a discussion of the main findings. Second, taking advantage of this first comprehensive dataset of soft-bodied meiofauna in an oceanic island, we assess the effects of biological and environmental variables on a set of predictors for meiofaunal diversity at two levels. (1) Regional level: we test the effect of biological variables on the number of soft-bodied meiofaunal endemic species found in the entire island. (2) Local level: we investigate the effect of environmental variables within the island, to test for differences in species richness, percentage of endemic species, and species composition across different types of habitats. At the regional level, we expect for example that groups with higher dispersal capabilities and smaller average size will have a lower percentage of endemic species in Lanzarote than other groups, as these traits are known to be associated to a more widespread distribution (Curini-Galletti et al. 2012). At the local level, we expect that the possibility for speciation events in isolated environments such as anchialine habitats and caves will be favoured; thus, a higher proportion of endemic species should be found in anchialine water bodies compared to the surrounding marine coastal environments.

Material and methods

Sampling localities

Between the 4th and 20th of October 2011, we sampled a total of 23 different localities in the island of Lanzarote, covering all types of marine, anchialine, and freshwater water bodies along the island and including habitats such as sandy beaches, pools, wells, caves, and open subtidal habitats (Fig. 1, Supplementary Table 1). Within each locality, which typically represented a single type of habitat (except for subtidal environments with caves, such as Mala, where two habitats were present), we sampled different substrates in order to obtain as many meiofaunal species as possible. Following this procedure, a total of 57 samples were collected, including sediments of different granulometry, mud, algae, and plankton tows from the water column. Sediments, mud, and algae were collected manually using plastic jars. We only collected the upper 5 cm of sediments, as this well-oxygenated layer contains the highest abundance of meiofauna (Higgins and Thiel 1988). Plankton tows were done only in the anchialine environments with a 100-μm mesh net, as 63-μm mesh nets are not efficient collecting fauna when towed by a diver (Iliffe, 2018). Freshwater and intertidal marine habitats were sampled on foot; subtidal habitats and anchialine caves were explored by scuba diving. Cave diving gear and techniques were employed within La Corona lava tube.

Soft-bodied meiofauna extraction and identification

Samples were taken to the laboratory soon after collection and processed within 1–2 days. Plankton tows were processed directly by siphoning off the water through a 63-μm mesh, in order to concentrate the fauna and get rid of the excess of water. Macroalgae samples were collected by hand, rinsed in $MgCl_2$, and squeezed into a 63-μm mesh before sorting out the meiofauna contained. Permeable sediments were processed daily using the $MgCl_2$ decantation technique, or by siphoning off the water just above the sediments (Higgins and Thiel 1988). Individual animals were identified alive by the specialist of each group participating in the workshop, and either fixed for detailed morphological studies or preserved in 100% ethanol for subsequent molecular analyses. We considered soft-bodied meiofauna in a broader sense and also included Priapula and Heterobranchia molluscs in our study, if they were smaller than a few millimetres. Despite ones having a moulting cuticle, and others epidermal spicules, these latter two groups of fragile animals share many traits of the soft-bodied group. We categorized as new species those that undoubtedly represented new species to science, while species with uncertain identity for which neither the status as new species nor an unambiguous identification could be performed we called doubtful. The latter ones typically included members of species complex, potential cryptic species, as well as immature and/or broken individuals showing unique traits. The total number of species recorded in the workshop are included in Table 1. A detailed description of the soft-bodied meiofaunal species obtained is provided in the first part of the manuscript.

Biological correlates of regional meiofaunal diversity

Our first goal was to investigate the effect and the importance of a set of biological variables, namely body size, dispersing capabilities, reproductive mode, and endobenthic preference, as predictors for endemism in island marine soft-bodied meiofauna. For analysing biogeographical patterns, small body size and the ecological consequences of being small are considered relevant as potentially favouring long-distance dispersal (Fontaneto 2019) and enabling widespread distribution according to the ubiquity theorem in microscopic animals (Fenchel and Finlay 2004). In both macrofauna and meiofauna, the presence of dispersal stages is known to affect endemism in many island groups (Ávila et al. 2012; Curini-Galletti et al. 2012), with taxa that are able to disperse through pelagic larval stages or dormant stages having widespread distributions. Considering reproductive mode, we expect parthenogenetic species to be able to establish a population after dispersal, even starting from a single individual, and therefore, we expect to find fewer endemic species amongst exclusively parthenogenetic species (Tilquin and Kokko 2016). We also expect to find a higher proportion of endemic species amongst endobenthic than amongst epibenthic species: endobenthic species are expected to have smaller distribution areas because they typically show adaptations to remain in the sediment (Bush 1968; Martin 1978), such as negative phototropism and adhesive glands, negatively affecting their dispersal capabilities (Curini-Galletti et al. 2012) (Table 2).

All data at the species level were merged in order to have one entry for each meiofaunal group, considering both the species found during the workshop as well as all the soft-bodied meiofaunal species previously found Lanzarote (Table 3). The proportion of endemic species for the Canary Islands for each group was calculated as including those species that are actually known as endemic plus those that are

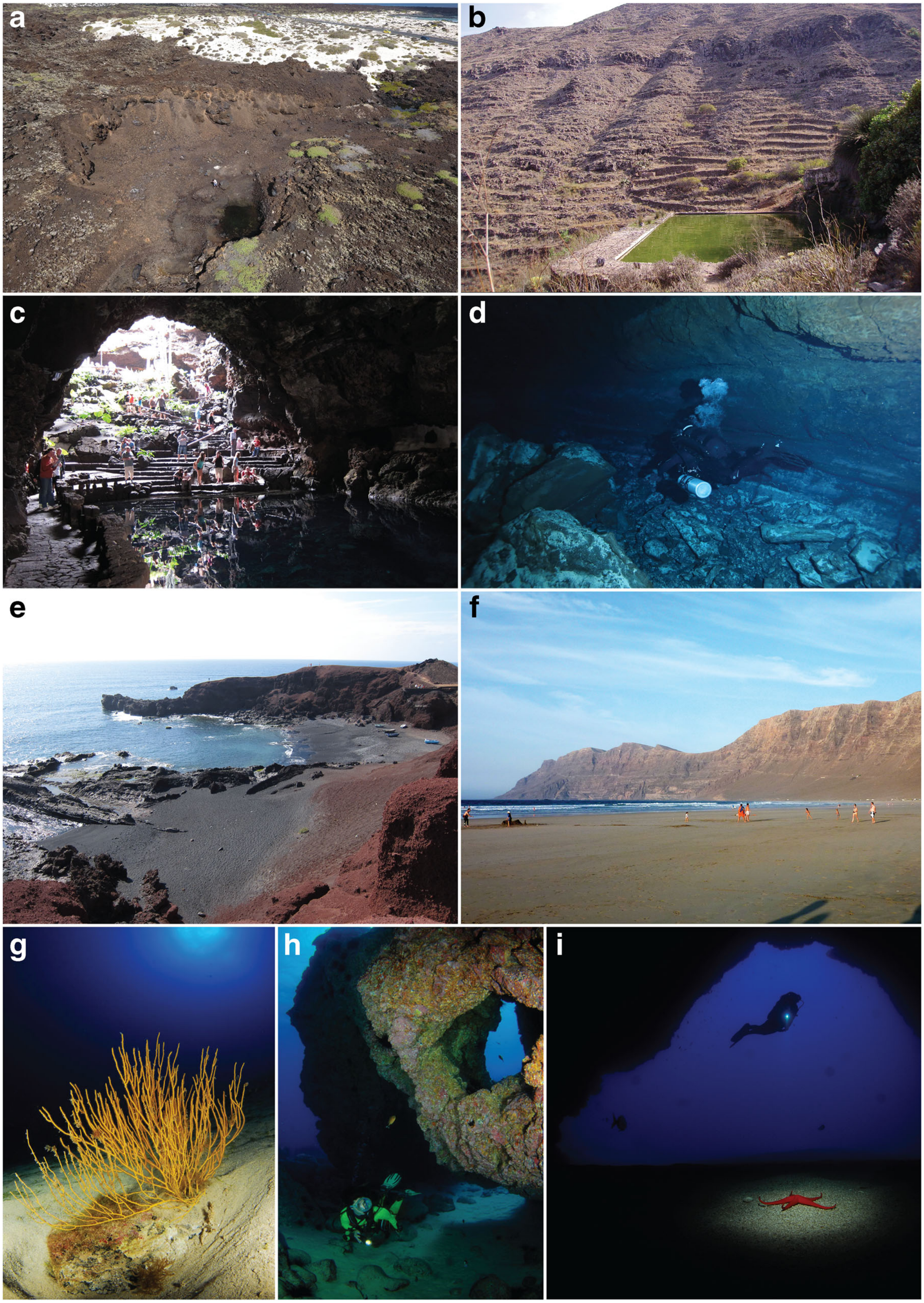

Fig. 1 Different types of localities sampled during the workshop, including **a** Charcos de Luis anchialine pools near Órzola; **b** freshwater reservoir in El Chafarís; **c** anchialine lake at Los Jameos del Agua; **d** Túnel de la Atlántida; **e** reflective beach in El Golfo; **f** dissipative beach in Famara; **g** Mala at 48 m; **h** La Catedral marine cave entrance; and **i** cuevita de Mala entrance (photo **a**, Gorka Leqclerq; **g**, **h**, **i**, Juan Valenciano)

Table 1 Checklist of soft-bodied meiofaunal taxa recorded in Lanzarote, along with the biological traits used in the analyses (see "Material and Methods"). The stations in which each species was found during the workshop were collected are summarized; a dash (−) in the station column indicates that the species is only recorded in the literature. A complete list of the sampled localities is included in Supplementary Table 1; for an exhaustive list of all soft-bodied meiofaunal taxa known from all of the Canary Islands, see Supplementary Table 2. Abbreviations: *unk*, unknown; *st*, station

Species	Size (mm)	Doubtful	New species	Endemic	Dispersal	Parthenogenetic	Endobenthic	Stations
Annelida								
Aeolosoma sp.	2	Yes	unk	unk	No	No	No	st. 45
Arenotrocha lanzarotensis Brito & Núñez, 2003	0.8	No	No	No	unk	No	Yes	–
cf. *Apodotrocha*	0.02	Yes	unk	unk	No	No	Yes	st. 10, st. 36
Claudrilus helgolandicus (Von Nordheim, 1983)	8	No	No	No	Yes	No	Yes	st. 10, st. 18, st. 19, st. 06, st. 09, st. 17, st. 48
Diurodrilus benazzi Gerlach, 1952	0.5	No	No	No	No	No	Yes	–
Dorvillea similis (Crossland, 1924)	1	No	No	No	Yes	No	No	–
Erinaceusyllis cryptica (Ben-Eliahu, 1977)	2	No	No	No	Yes	No	No	–
Exogone breviantennata Hartmann-Schröder, 1959	3	No	No	No	Yes	No	No	–
Exogone gambiae Lanera, Sordino & San Martín, 1994	3.5	No	No	No	Yes	No	No	–
Exogone meridionalis Cognetti, 1955	1.5	No	No	No	Yes	No	No	–
Fauveliopsis glabra (Hartman, 1960)	3.8	No	No	No	No	No	Yes	st. 32
Fauveliopsis jameoaquensis Núñez, 1997	0.8	No	No	Yes	No	No	Yes	st. 24
Hesionides arenaria Friedrich, 1937	1.5	No	No	No	No	No	Yes	st. 28
Hesionura elongata (Southern, 1914)	1.5	No	No	No	No	No	Yes	st. 10, st. 29
Laubierpholoe sp.	3	No	Yes	Yes	No	No	Yes	st. 24, st. 25, st. 43
Leptonerilla diatomeophaga Núñez, 1997	1.2	No	No	Yes	No	No	Yes	st. 24, st. 25
Levinsenia canariensis (Brito & Núñez, 2002)	6	No	No	No	Yes	No	Yes	–
Lindrilus sp.	9	No	Yes	Yes	Yes	No	Yes	st. 36
Macrochaeta n. sp. in Núñez, 1997	0.9	No	No	Yes	No	No	Yes	st. 24
Macrochaeta sp. 3	1.5	No	Yes	Yes	No	No	Yes	st. 06
Megadrilus pelagicus Martinez, Kvindebjerg, Iliffe & Worsaae, 2016	17.7	No	No	Yes	No	No	No	st. 47, st. 22
Megadrilus schneideri (Langerhans, 1880)	17	No	No	No	Yes	No	Yes	st. 30, st. 32, st. 36
Meganerilla cesari Worsaae, Martinez & Nunez, 2009	1	No	No	Yes	No	No	Yes	st. 05
Meiodrilus sp. 1 (in Martinez et al. 2015)	4	No	Yes	Yes	Yes	No	Yes	st. 01
Meiodrilus sp. 4 (in Martinez et al. 2015)	6	No	Yes	Yes	Yes	No	Yes	st. 29
Mesonerilla armoricana Swedmark, 1959	1.1	No	No	No	No	No	Yes	st. 05, st. 06, st. 19
Mesonerilla cf. *luederitzi*	1	No	Yes	Yes	No	No	Yes	st. 06, st. 09, st. 16, st. 47, st. 48
Mesonerilla laerkae Worsaae, Mikkelsen & Martínez, 2019a	0.8	No	Yes	Yes	No	No	Yes	st. 05, st. 19
Mesonerilla xurxoi Worsaae, Mikkelsen & Martínez, 2019a	0.8	No	Yes	Yes	No	No	No	st. 05, st. 24, st. 25
Miscellania dentanta Martín, Alós & Sardá, 1990	1.6	No	No	No	No	No	Yes	st. 05, st. 24, st. 25
Nerillidium gracile Remane, 1925	0.5	No	No	No	No	No	Yes	st. 22
Nerillidium sp.	0.5	Yes	unk	unk	No	No	Yes	st. 05, st. 16, st. 24
Nerillidium troglochaetoides Remane, 1925	0.5	No	No	No	No	No	Yes	st. 09
Ophryotrocha labronica Bacci & La Greca, 1962	3	No	No	No	Yes	No	No	–
Ophryotrocha paragerlachi Brito & Núñez, 2003	0.6	No	No	No	Yes	No	No	–
Ophryotrocha splendida Brito & Núñez, 2003	0.8	No	No	No	Yes	No	No	–
Paradoneis armata Glémarec, 1966	35	No	No	No	Yes	No	No	–
Paradoneis lyra (Southern, 1914)	13.4	No	No	No	Yes	No	Yes	–
Paradoneis perdidoensis (McLelland & Gaston, 1994)	3.5	No	No	No	Yes	No	Yes	–
Parapionosyllis elegans (Pierantoni, 1903)	2	No	No	No	Yes	No	Yes	–
Parapionosyllis labronica Cognetti, 1965	3.5	No	No	No	Yes	No	Yes	–
Parapionosyllis macaronesiensis Brito, Núñez & San Martín, 2000	3	No	No	No	Yes	No	Yes	–
Parexogone hebes (Webster & Benedict, 1884)	10	No	No	No	Yes	No	No	–
Perkinsyllis spinisetosa (San Martin, 1990)	8	No	No	No	Yes	No	No	–
Pharygocirrus cf. *gabrielae*	7	Yes	unk	unk	Yes	No	Yes	st. 39
Pisione guanche San MartÌn, Lopez & Nunez, 1999	4	No	No	No	Yes	No	Yes	st. 36

Table 1 (continued)

Species	Size (mm)	Doubtful	New species	Endemic	Dispersal	Parthenogenetic	Endobenthic	Stations
Polygordius sp.	4.5	Yes	unk	unk	Yes	No	Yes	st. 06
Prosphaerosyllis campoyi (San Martín, Acero, Contonente & Gomez, 1982)	1.5	No	No	No	Yes	No	No	–
Protodorvillea kefersteini (McIntosh, 1869)	15	No	No	No	Yes	No	No	–
Protodrilus cf. *hatscheki*	12	Yes	unk	unk	Yes	No	Yes	st. 36
Psammodrilus sp. in Worsaae, Giribet & Martínez, 2018	0.5	No	Yes	Yes	No	No	Yes	st. 16
Questa caudicirra Hartman, 1966	10	No	No	No	unk	No	Yes	–
Questa cf. *riseri*	10	No	Yes	Yes	No	No	Yes	st. 05, st. 10
Raphidrilus nemasoma Monticelli, 1910	7	No	No	No	Yes	No	Yes	st. 12, st. 16
Saccocirrus parvus Gerlach, 1953	13	No	No	No	Yes	No	Yes	st. 30
Salvatoria limbata (Claparède, 1868)	3	No	No	No	Yes	No	No	–
Salvatoria vieitezi (San Martín, 1984)	1.5	No	No	No	Yes	No	No	–
Speleonerilla isa Worsaae et al., 2019b	0.58	No	Yes	Yes	No	No	No	st. 47, st. 22
Sphaerosyllis austriaca Banse, 1959	2	No	No	No	Yes	No	No	–
Sphaerosyllis hystrix Claparède, 1863	5	No	No	No	Yes	No	No	–
Sphaerosyllis taylori Perkins, 1981	3	No	No	No	Yes	No	No	–
Streptodonta pterochaeta (Southern, 1914)	6	No	No	No	Yes	No	No	–
Streptosyllis bidentata Southern, 1914	2.5	No	No	No	Yes	No	Yes	–
Streptosyllis campoyi Brito, Núñez & San Martín, 2000	2	No	No	No	Yes	No	Yes	–
Streptosyllis websteri Southern, 1914	3.5	No	No	No	Yes	No	No	–
Syllides fulvus (Marion & Bobretzky, 1875)	2.5	No	No	No	Yes	No	No	–
Syllides japonicus Imajima, 1966	7	No	No	No	Yes	No	No	–
Trochonerilla sp.	0.8	No	Yes	Yes	No	No	Yes	st. 36
Cnidaria: Actinulida								
Halammohydra sp.	0.5	Yes	unk	unk	No	No	Yes	st. 09a, st. 09b, st. 09c, st. 10, st. 16, st. 37
Otohydra sp.	0.5	Yes	unk	unk	No	No	Yes	st. 10, st. 11
Gastrotricha								
Acanthodasys aculeatus Remane, 1927	0.6	No	No	No	No	No	Yes	st. 13
Acanthodasys sp. 1	0.33	No	Yes	Yes	No	No	Yes	st. 10
Aspidiophorus marinus Remane, 1926	0.17	No	No	No	No	Yes	Yes	st. 01, st. 10, st. 27
Aspidiophorus paramediterraneus Hummon, 1974	0.26	No	No	No	No	Yes	Yes	st. 01, st. 10, st. 18
Aspidiophorus sp. 1	0.2	Yes	unk	unk	No	Yes	Yes	st. 10
Aspidiophorus sp. 2	0.26	No	Yes	No	No	Yes	Yes	st. 35
Aspidiophorus sp. 3	0.2	Yes	unk	unk	No	Yes	Yes	st. 10
Cephalodays sp. 1	0.45	Yes	unk	unk	No	No	Yes	st. 30, st. 32
Chaetonotus apechochaetus Hummon, Balsamo & Todaro, 1992	0.11	No	No	No	No	Yes	Yes	st. 16
Chaetonotus apolemmus Hummon, Balsamo & Todaro, 1992	0.13	No	No	No	No	Yes	Yes	st. 01, st. 17, st. 29
Chaetonotus dispar Wilke, 1954	0.11	No	No	No	No	Yes	Yes	st. 18, st. 29
Chaetonotus lacunosus Mock, 1979	0.13	No	No	No	No	Yes	Yes	st. 18
Chaetonotus neptuni Wilke, 1954	0.19	No	No	No	No	Yes	Yes	st. 10
Chaetonotus siciliensis Hummon, Balsamo & Todaro, 1992	0.2	No	No	No	No	Yes	Yes	st. 17
Chaetonotus sp. 1	0.13	No	Yes	No	No	Yes	Yes	st. 01, st. 13, st. 16
Chaetonotus sp. 2	0.11	Yes	unk	unk	No	Yes	Yes	st. 29
Chaetonotus variosquamatus Mock, 1979	0.1	No	No	No	No	Yes	Yes	st. 29
Crasiella sp. 1	0.51	Yes	unk	unk	No	No	Yes	st. 01, st. 16
Dactylopodola typhle (Remane, 1927)	0.38	No	No	No	No	No	Yes	st. 01, st. 29, st. 30
Dendrodasys sp. 1	0.24	Yes	unk	unk	No	No	Yes	st. 37
Diplodasys minor Remane, 1936 sensu Todaro, 1992	0.3	No	No	No	No	No	Yes	st. 01
Diplodasys sp. 1	0.3	Yes	unk	unk	No	No	Yes	st. 01, st.7
Diplodasys sp. 2	0.28	Yes	unk	unk	No	No	Yes	st. 10, st. 16
Diplodasys sp. 3	0.57	Yes	unk	unk	No	No	Yes	st. 16
Draculiciteria tesselata (Renaud Mornant, 1968)	0.24	No	No	No	No	Yes	Yes	st. 29
Halichaetonotus aculifer (Gerlach, 1953)	0.16	No	No	No	No	Yes	Yes	st. 18
Halichaetonotus decipiens (Remane, 1929)	0.08	No	No	No	No	Yes	Yes	st. 29
Halichaetonotus paradoxus (Remane, 1927)	0.15	No	No	No	No	Yes	Yes	st. 18

Table 1 (continued)

Species	Size (mm)	Doubtful	New species	Endemic	Dispersal	Parthenogenetic	Endobenthic	Stations
Halichaetonotus sp. 1	0.1	Yes	unk	unk	No	Yes	Yes	st. 29
Heterolepidoderma loricatum Schrom, 1972	0.11	No	No	No	No	Yes	Yes	st. 18
Heteroxenotrichula pygmaea (Remane, 1934)	0.19	No	No	No	No	Yes	Yes	st. 37
Heteroxenotrichula sp. 1	0.25	Yes	unk	unk	No	No	Yes	st. 37
Lepidodasys martini Remane, 1926	0.59	No	No	No	No	No	Yes	st. 37
Lepidodasys platyurus Remane, 1927	0.51	No	No	No	No	No	Yes	st. 32
Lepidodasys sp. 1	0.42	No	Yes	Yes	No	No	Yes	st. 10
Lepidodasys unicarenatus Balsamo, Fregni & Tongiorgi, 1994	0.45	No	No	No	No	No	Yes	st. 10
Macrodasys sp. 1	0.68	Yes	unk	unk	No	No	Yes	st. 01, st. 07
Macrodasys sp. 2	0.56	Yes	unk	unk	No	No	Yes	st. 01
Macrodasys sp. 3	0.67	Yes	unk	unk	No	No	Yes	st. 01
Macrodasys sp. 4	0.68	Yes	unk	unk	No	No	Yes	st. 16
Megadasys sterreri (Boaden, 1974)	1.3	No	No	No	No	No	Yes	st. 13, st. 16
Mesodasys laticaudatus Remane, 1951	0.95	No	No	No	No	No	Yes	st. 01, st. 05, st. 13, st. 16, st. 17
Musellifer delamarei (Renaud-Mornant, 1968)	0.19	No	No	No	No	No	Yes	st. 10, st. 29
N. gen et n. sp.	0.39	No	Yes	Yes	No	No	Yes	st. 32
Neodasys sp. 1	0.39	Yes	unk	unk	No	No	Yes	st. 18
Oregodasys cirratus Rothe & Schmidt-Rhaesa, 2010	0.52	No	No	Yes	No	No	Yes	st. 34, st. 36
Oregodasys sp. 1	0.29	Yes	unk	unk	No	No	Yes	st. 01
Paraturbanella dorhni Remane, 1927	0.41	No	No	No	No	No	Yes	st. 37
Paraturbanella pallida Luporini, Magagnini & Tongiorgi, 1973	0.59	No	No	No	No	No	Yes	st. 01, st. 16
Pseudostomella sp. 1	0.21	Yes	unk	unk	No	No	Yes	st. 29
Ptychostomella mediterranea Remane, 1927	0.18	No	No	No	No	No	Yes	st. 01, st. 37
Ptychostomella sp. 1	0.15	No	Yes	Yes	No	No	Yes	st. 17
Tetranchyroderma canariense Todaro et al. 2003	0.41	No	No	Yes	No	No	Yes	st. 01, st. 10, st. 16
Tetranchyroderma cirrophorum Lévi, 1950	0.55	No	No	No	No	No	Yes	st. 17
Tetranchyroderma sp. 1	0.2	Yes	unk	unk	No	No	Yes	st. 01
Tetranchyroderma sp. 2	0.49	No	Yes	Yes	No	No	Yes	st. 16, st. 37
Thaumastoderma mediterraneum Remane, 1927	0.15	No	No	No	No	No	Yes	st. 01, 10
Urodasys acanthostylis Fregni, Tongiorgi & Faienza, 1998	0.34	No	No	No	No	No	Yes	st. 32
Urodasys completus Todaro, Cesaretti & Dal Zotto, 2019a	0.3	No	Yes	Yes	No	No	Yes	st. 32
Urodasys mirabilis Remane, 1926	0.63	No	No	No	No	No	Yes	st. 01, st. 10, st. 13, st. 16
Xenotrichula punctata Wilke, 1954	0.24	No	No	No	No	No	Yes	st. 01, st. 13, st. 16
Gnathostomulida								
Austrognathia sp.	1	Yes	unk	unk	No	No	No	st. 05, st. 13, st. 16
Mollusca: Heterobranchia								
Helminthope sp. 1	0.7	No	Yes	Yes	No	No	Yes	st. 22
Helminthope sp. 2	2.5	No	Yes	Yes	No	No	Yes	st. 36
Helminthope sp. 3	4	No	Yes	Yes	No	No	Yes	st. 50
Pontohedyle milaschewitchii (Kowalevsky, 1901)	4	No	No	No	Yes	No	Yes	st. 32
Nemertea								
Nemertopsis sp.	3	Yes	unk	unk	Yes	No	No	st. 48
Ototyphlonemertes duplex D04 in Leasi, Andrade & Norenburg, 2016	11	No	Yes	No	Yes	No	Yes	NA
Ototyphlonemertes duplex D05 in Leasi, Andrade & Norenburg, 2016	6	No	Yes	Yes	Yes	No	Yes	NA
Ototyphlonemertes santacruzensis S04 in Leasi, Andrade & Norenburg, 2016	5	No	Yes	No	Yes	No	Yes	st. 50
Cephalotryx sp. 1	25	No	No	No	Yes	No	No	st. 40
Cephalotryx sp. 2	10	No	No	No	Yes	No	No	st. 40
Platyhelminthes: Proseriata								
Archilina coronata Curini-Galletti, Casu & Scarpa, 2019 (Scarpa et al. 2019b)	1.5	No	Yes	Yes	No	No	Yes	st. 03, st. 06, st. 09, st. 10, st. 12, st. 15, st. 16, st. 32, st. 33, st. 35, st. 36

Table 1 (continued)

Species	Size (mm)	Doubtful	New species	Endemic	Dispersal	Parthenogenetic	Endobenthic	Stations
Archilina regina Curini-Galletti, Casu & Scarpa, 2019 (Scarpa et al. 2019b)	1.5	No	Yes	Yes	No	No	Yes	st. 10, st. 12, st. 15, st. 16, st. 32, st. 33, st. 35
Archimonocelis sp. I	3	No	Yes	Yes	No	No	Yes	st. 09
Archimonocelis sp. II	3	No	Yes	Yes	No	No	Yes	st. 01, st. 41
Archimonocelis sp. III	3	No	Yes	Yes	No	No	Yes	st. 06
Archimonocelis sp. IV	3	No	Yes	Yes	No	No	Yes	st. 10, st. 11, st. 12, st. 15, st. 16, st. 17
Archimonocelis sp. V	3	No	Yes	Yes	No	No	Yes	st. 37
Archimonocelis sp. VI	3	No	Yes	Yes	No	No	Yes	st. 05
Boreocelis sp.	2	No	Yes	Yes	No	No	Yes	st. 05, st. 12, st. 15, st. 16, st. 17, st. 32
Duplominona sp. I	1.5	No	Yes	Yes	No	No	Yes	st. 01, st. 12, st. 15, st. 16, st. 17, st. 21
Duplominona sp. II	1.5	No	Yes	No	No	No	Yes	st. 05, st. 10, st. 12, st. 15, st. 16, st. 17, st. 32
Duplominona sp. III	1.5	No	Yes	Yes	No	No	Yes	st. 06, st. 12, st. 15, st. 16, st. 17
Invenusta sp.	3	No	Yes	Yes	No	No	Yes	st. 21
Minona sp. I	1	No	Yes	Yes	No	No	Yes	st. 12, st. 15, st. 16, st. 17
Minona sp. II	1	no	Yes	Yes	No	No	Yes	st. 32
Minona sp. III	1.5	no	Yes	Yes	No	No	Yes	st. 05
Monocelidid sp. 40	1	Yes	unk	unk	No	No	Yes	st. 12, st. 15
Monocelidid sp. 50	1	Yes	unk	unk	No	No	Yes	st. 32
Monocelis longistyla Martens & Curini-Galletti, 1987	1.5	No	No	No	No	No	Yes	st. 01
Monocelis sp. I	1.5	No	Yes	No	No	No	Yes	st. 41
Monocelis sp. II	1.5	No	Yes	Yes	Yes	No	NA	st. 6, st. 27
Monostichoplana 'filum mediterranea'	3	No	Yes	No	No	No	Yes	st. 29, st. 46
Monostichoplana sp. I	4	No	Yes	Yes	No	No	Yes	st. 36
Monotoplana sp.	1.5	No	Yes	No	Yes	No	No	st. 32
Otoplana didomenicoi Curini-Galletti, Scarpa & Casu, 2019 (Scarpa et al. 2019a)	2	No	Yes	No	No	No	Yes	st. 28
Parotoplana sp. I	2	No	Yes	Yes	No	No	Yes	st. 01
Parotoplana sp. II	2	No	Yes	Yes	No	No	Yes	st. 01
Parotoplana sp. III	1.5	No	Yes	Yes	No	No	Yes	st. 01, st. 29
Parotoplana sp. IV	2	No	Yes	Yes	No	No	Yes	st. 13, st. 18
Parotoplana sp. V	2	No	Yes	Yes	No	No	Yes	st. 06, st. 36, st. 43
Parotoplana sp. VI	2	No	Yes	Yes	No	No	Yes	st. 01, st. 16
Parotoplana sp. VII	2	No	Yes	No	No	No	Yes	st. 06
Polystyliphora cf. *filum*	3	Yes	unk	unk	No	No	Yes	st. 12, st. 32, st. 33, st. 35
Polystyliphora sp. I	3	No	Yes	No	No	No	Yes	st. 48
Polystyliphora sp. II	3	No	Yes	No	No	No	Yes	st. 36
Pseudorthoplana cf. *foliacea*	3	Yes	unk	unk	No	No	Yes	st. 16
Vannuccia campana Ehlers & Ehlers, 1980	3	No	No	No	No	No	Yes	st. 01, st. 05, st. 14
Vannuccia sp. I	4	No	Yes	Yes	No	No	Yes	st. 09, st. 12, st. 15, st. 16, st. 17
Vannuccia sp. II	4	No	Yes	Yes	No	No	Yes	st. 12, st. 15, st. 17
Platyhelminthes: Rhabdocoela								
Brunetorhynchus canariensis Schockaert, Janssen & Artois, 2014	0.7	No	Yes	Yes	No	No	Yes	st. 10, st. 37
Brunetorhynchus microstylis Schockaert, Revis & Artois, 2014	0.8	No	Yes	No	No	No	Yes	st. 10, st. 37
Carcharodorhynchus flavidus Brunet, 1967	1.7	No	No	No	No	No	Yes	st. 06, st. 09a, st. 10, st. 16, st. 36, st. 37
Carcharodorhynchus sp. 2	unk	Yes	unk	unk	No	No	Yes	st. 06, st. 16, st. 37
Carcharodorhynchus worsaae Reygel, Janssen & Artois, 2014	1.2	No	Yes	Yes	No	No	Yes	st. 06, st. 13
Ceratopera sellai (Steinböck, 1933) Den Hartog, 1964	1.5	No	No	No	No	No	No	st. 26, st. 27

Table 1 (continued)

Species	Size (mm)	Doubtful	New species	Endemic	Dispersal	Parthenogenetic	Endobenthic	Stations
Cheliplana canariensis Gobert, Reygel & Artois, 2019	0.6	No	Yes	Yes	No	No	Yes	st. 37
Cheliplana curini Gobert, Reygel & Artois, 2019	1.0	No	Yes	No	No	No	Yes	st. 10, st. 13, st. 16
Cheliplana sarnsis Gobert, Reygel & Artois, 2019	1.0	No	Yes	Yes	No	No	No	st. 13, st. 16, st. 17, st. 26, st. 29
Cheliplana sp. 4	unk	Yes	unk	unk	No	No	Yes	st. 10, st. 37
Cheliplana sp. 5	unk	Yes	unk	unk	No	No	Yes	st. 10
Cheliplana sp. 6	unk	Yes	unk	unk	No	No	Yes	st. 10
Cheliplanilla cavavulcana Gobert, Reygel & Artois, 2019	1.4	No	Yes	Yes	No	No	Yes	st. 05
Cheliplanilla todaroi Gobert, Reygel & Artois, 2019	1.0	No	Yes	Yes	No	No	Yes	st. 10
Cicerinide sp.	unk	Yes	unk	unk	No	No	Yes	st. 37
Coronhelmis sp.	unk	Yes	unk	unk	No	No	Yes	st. 30
Cystiplex(?) sp.	unk	No	Yes	Yes	No	No	Yes	st. 06, st. 09a, st. 10, st. 30, st. 34, st. 36, st. 37, st. 39
Cystirete graefei Brunet, 1965	1.5	No	No	No	No	No	Yes	st. 09a
Dalyellioide sp.	unk	Yes	unk	unk	No	No	Yes	st. 46
Drepanorhynchides sp.	unk	Yes	unk	unk	No	No	Yes	st. 05, st. 36
Gnathorhynchide sp.	unk	Yes	unk	unk	No	No	Yes	st. 37
Gyratrix hermaphroditus Ehrenberg, 1831	1.0	No	No	No	No	No	No	st. 06, st. 07, st. 16, st. 26, st. 27, st. 30, st. 36, st. 37, st. 41
Gyratrix proavus Meixner, 1938	1.0	No	No	No	No	No	Yes	st. 10
Itaipusa sp.	unk	Yes	unk	unk	No	No	Yes	st. 06, st. 07
Kaitalugia cfr. *falcata*	0.5	Yes	unk	unk	No	No	No	st. 26
Kytorhynchid sp.	unk	No	Yes	Yes	No	No	Yes	st. 06, st. 09a, st. 30
Kytorhynchid sp. 2	unk	No	Yes	Yes	No	No	Yes	st. 09a
Lagenopolycystis sp.	unk	No	Yes	Yes	No	No	No	st. 06, st. 09a, st. 10, st. 16, st. 26, st. 30, st. 36, st. 37
Limipolycystis sp.	unk	Yes	unk	unk	No	No	Yes	st. 19
Maehrenthallia?	unk	Yes	unk	unk	No	No	Yes	st. 03
Mariplanella sp.	unk	No	Yes	Yes	No	No	Yes	st. 06, st. 09a
Messoplana cf. *falcata*	unk	Yes	unk	unk	No	No	Yes	st. 06, st. 10, st. 16, st. 17, st. 37
Nannorhynchides	unk	Yes	unk	unk	No	No	No	st. 26, st. 27
Paraustrorhynchus sp.	unk	No	Yes	Yes	No	No	No	st. 26
Paulodora sp.	unk	No	Yes	Yes	No	No	No	st. 06, st. 09a, st. 26
Paulodora sp. 2	unk	No	Yes	Yes	No	No	No	st. 26
Polycystide cf. *neopolycystis*	unk	No	Yes	Yes	No	No	Yes	st. 46
Polycystidid nov. gen.	unk	No	Yes	Yes	No	No	Yes	st. 06, st. 46
Polycystis naegelii Kolliker, 1845	1.2	No	No	No	No	No	No	st. 26
Progyrator cf. *mamertinus*	0.8	Yes	unk	unk	No	No	Yes	st. 13
Promesostoma sp.	unk	No	Yes	Yes	No	No	Yes	st. 16, st. 37
Promesostoma sp. 2	unk	No	Yes	Yes	No	No	Yes	st. 37
Promesostomid sp.	unk	Yes	unk	unk	No	No	Yes	st. 06, st. 17
Promesostomid sp. 2	unk	Yes	unk	unk	No	No	Yes	st. 17
Promesostomid sp. 3	unk	Yes	unk	unk	No	No	Yes	st. 37
Promesostomid sp. 4	unk	Yes	unk	unk	No	No	Yes	st. 37
Proschizorhynchella? sp.	unk	Yes	unk	unk	No	No	Yes	st. 16, st. 37
Proschizorhynchus martinezi Gobert, Reygel & Artois, 2019	1.7	No	Yes	Yes	No	No	Yes	st. 01, st. 05, st. 15
Pseudoschizorhynchoides timoshkini Gobert, Reygel & Artois, 2019	1.8	No	Yes	Yes	No	No	Yes	st. 05, st. 06, st. 09a
Rogneda sp.	unk	No	Yes	Yes	No	No	Yes	st. 06, st. 13
Rogneda sp. 2	unk	No	Yes	Yes	No	No	Yes	st. 37
Rogneda sp. 3	unk	No	Yes	Yes	No	No	Yes	st. 37
Rogneda reticulata (?)	unk	Yes	unk	unk	No	No	Yes	st. 37
Schizochilus lanzarotensis Gobert, Reygel & Artois, 2019	unk	No	Yes	Yes	No	No	Yes	st. 05

Table 1 (continued)

Species	Size (mm)	Doubtful	New species	Endemic	Dispersal	Parthenogenetic	Endobenthic	Stations
Solenopharyngidae sp. 1	unk	Yes	unk	unk	No	No	Yes	st. 09a
Solenopharyngidae sp. 2	unk	Yes	unk	unk	No	No	Yes	st. 37
Trigonostomid sp.	unk	Yes	unk	unk	No	No	No	st. 26
Trigonostomid sp. 2	unk	Yes	unk	unk	No	No	No	st. 26
Trigonostomum sp.	unk	No	Yes	Yes	No	No	No	st. 26
Trigonostomum sp. 2	unk	No	Yes	Yes	No	No	Yes	st. 10
Trigonostomum penicillatum (Schmidt, 1857) Micoletzky, 1910	1.2	No	No	No	No	No	No	st. 26
Typhloplanide sp. 1	unk	Yes	unk	unk	No	No	Yes	st. 05
Typhloplanide sp. 2 *(Kymocarens?)*	unk	Yes	unk	unk	No	No	Yes	st. 05
Typhloplanide sp. 3 *(Haloplanella??)*	unk	Yes	unk	unk	No	No	Yes	st. 10, st. 37
Typhloplanoide sp.	unk	Yes	unk	unk	No	No	Yes	st. 05, st. 06
Typhloplanoide sp. 2	unk	Yes	unk	unk	No	No	No	st. 26
Typhloplanoide sp. 3	unk	yes	unk	unk	No	No	Yes	st. 10, st. 37
Typhlopolycystis pluvialiae Schockaert, Janssen & Artois, 2019	1.0	No	Yes	Yes	No	No	Yes	st. 10
Typhlopolycystis sarda Artois, Moons & Schockaert, 2019	1.0	No	Yes	No	No	No	Yes	st. 37
Uncinorhynchus sp.	unk	Yes	unk	unk	No	No	Yes	st. 01
Utelga cf. *pseudoheinckei*	unk	Yes	unk	unk	No	No	No	st. 10, st. 26
Utelga sp.	unk	Yes	unk	unk	No	No	Yes	st. 06, st. 07, st. 09a, st. 16, st. 17
Utelga sp. 2 *(Neoutelga)*	uk	Yes	unk	unk	No	No	Yes	st. 34
Priapulida								
Tubiluchus lemburgi Schmidt-Rhaesa, Rothe & Martínez, 2013	0.95	No	No	Yes	No	No	Yes	st. 05, st. 17, st. 32, st. 43
Rotifera								
Philodina megalotrocha Ehrenberg, 1832	0.4	No	No	No	Yes	Yes	No	A829
Philodina roseola Ehrenberg, 1832	0.4	No	No	No	Yes	Yes	No	A829
Rotaria rotatoria	0.3	No	No	No	Yes	Yes	No	st.06, A822; A829, A832
Rotaria sp.	0.3	Yes	unk	unk	Yes	Yes	No	st. 32, st. 36
Brachionus sp. 1 small	0.2	Yes	unk	unk	No	Yes	No	A829
Brachionus sp. 2 large	0.4	Yes	unk	unk	No	Yes	No	A829
Brachionus sp. 3 regular	0.3	Yes	unk	unk	No	Yes	No	A832
Colurella sp.	0.1	Yes	unk	unk	no	Yes	No	st. 09c, st. 37, A822, A827
Encentrum sp.	0.2	Yes	unk	unk	No	Yes	No	A822, A830, st.42
Filinia sp.	0.25	Yes	unk	unk	No	Yes	No	A832
Lepadella sp.	0.15	Yes	unk	unk	No	Yes	No	A830
Proales sp. 1 small	0.1	Yes	unk	unk	No	Yes	No	A822, A823, A825, A834, A835, A836, A837, st. 27, st. 42
Proales sp. 2 large	0.3	Yes	unk	unk	No	Yes	NA	st. 06
Testudinella sp.	0.2	No	Yes	Yes	No	Yes	No	A822, A823, st. 06, st. 09, st. 10, st. 32, st. 09c, st. 36, st. 37
Testudinella sp. round	0.2	Yes	unk	unk	No	Yes	NA	st. 36, st. 37

new species to science, which, being unknown anywhere else, are potentially endemic. The few species new to science found in Lanzarote that were subsequently found elsewhere outside the Canary Islands were excluded from the count of endemic species.

Explanatory variables that could affect the proportion of endemic species included body size, dispersal potential, reproductive mode, and substrate specificity. An estimate of body size (median body length) for each species was obtained from the adult individuals collected in the field and/or from literature data. Potential for dispersal was estimated by collecting information on the presence/absence of larval and resting or dispersing stages, including cysts, dormant embryos, resting eggs, and epitokous reproductive stages. For reproductive mode, we categorized organisms as exclusively parthenogenetic or not. For habitat specificity, species were grouped as exclusively endobenthic (either as interstitial or burrower) or not.

We investigated the relative importance of each of these variables using generalized linear models, including the proportion of endemic species for each meiofaunal group as a response variable and all four biological predictors as explanatory variables. A binomial distribution was assumed, as the response variable was proportion data. The significance and importance of each explanatory variable were evaluated using model averaging (Burnham et al. 2002). The relevance of the results will be based on the relative importance values from model averaging and on *p* values. Model averaging and relative importance of the explanatory variables were calculated with the package *MuMIn* v. 1.15.6 (Bartoń 2016) of the statistic software R v. 3.5.0 (Team, 2013).

Environmental correlates of local meiofaunal diversity

Our second goal was to investigate the effect of environmental differences on the occurrence of endemic species, focusing at a local level of different habitat. We used species richness (i.e. number of species), percentage of endemic species (i.e. proportion of species only found in the Canary Islands and considered as actually or potentially endemic), and differences in species composition across sampling sites as response variables against a set of environmental parameters. For these analyses, we focused only on saltwater habitats and disregarded freshwater habitat in order to avoid the statistical confounding factors of several groups that are not present or were not searched in freshwater habitats.

In saltwater habitats, we expect differences between anchialine and marine environments, between type of habitat (i.e. sandy beaches, ponds, caves, and subtidal habitats), and between type of substrate (i.e. mud, sand, algae, water column) would affect communities of microscopic animals. Anchialine environments in Lanzarote are known to harbour fewer species, but have a higher percentage of endemic species, with different communities than marine waters, especially in terms of crustaceans (Martínez et al. 2009). Thus, we expect that differences between anchialine and marine environments may have a strong effect also on meiofauna, in terms of species richness, percentage of endemic species, and species composition. Regarding type of habitat and type of substrate, we have no a priori expectations, except that differences in habitat and substrate may differentially affect meiofauna.

Richness and percentage of endemic species were investigated for the total meiofauna, as well as separately for groups with more than ten species (Annelida, Gastrotricha, Proseriata, and Rhabdocoela). As explanatory variables, we considered three factors: environment (two levels: anchialine, marine), habitat (four levels: cave, beach, pond, subtidal), and substrate (four levels: algae, mud, sediment, water). We used analysis of variance (AnoVA), implemented in R, to investigate the differences in species richness and endemism. Richness was measured as number of species, which is count data and therefore was transformed to its logarithm in the models; the proportion of endemic species for each community varied between 0 and 1, and given that this distribution is bound at the two extremes, it was transformed using the arcsine of the square root (Crawley 2012). We checked model fit by visually confirming the normal distribution of the residuals, the absence of deviation in the residual versus fitted plot, Q-Q plot, and plot of Cook's distances.

Differences in meiofauna community composition were investigated using the Jaccard similarity index (Jaccard 1901; Chao et al. 2012) calculated for the total meiofauna and separately for the groups with more than ten species (Annelida, Gastrotricha, Proseriata, and Rhabdocoela). The explanatory variables were the same for the richness models. We used a permutational multivariate analysis of variance to investigate the differences in species composition, using the R package *vegan* v. 2.5.2 (Oksanen et al. 2017), since the response variable was a matrix of pairwise distances.

Results

Overview of meiofaunal diversity of Lanzarote

We recorded a total of 239 species, 86 of them undescribed and new to science and 81 with uncertain identity (Fig. 2). Amongst the 86 undescribed species, 11 were already known or subsequently found also outside of the Canary Islands. The total number of endemic species was 88, including 7 known only from the Canary Islands, and therefore considered actually endemic, together with 75 new species for science that have not been found anywhere else so far, and therefore are considered potentially endemic. From these potentially endemic species, 13 are described in this special issue and can be considered actually endemic (Di Domenico et al. 2019; Gobert et al., 2019; Scarpa et al., 2019a, b; Todaro et al., 2019a; Worsaae et al., 2019a, b), while 5 were described elsewhere (Reygel et al. 2014; Schockaert et al. 2014; 2019). Out of the 239 total species, 135 species are new records from the Canary Islands. We here provide an overview on the results for all the recorded, in alphabetical order.

The 81 doubtful, unidentified species will be used in the following analyses together with the total number of species, assuming that they were not endemic, in order to use only the most consistent estimate of endemic species in the inference.

Annelida Annelida is an animal phylum with more than 17,000 described species colonizing all types of aquatic and terrestrial environments. More than 400 meiofaunal species are found across 25 families, with 11 of these being exclusively meiofaunal or interstitial. Since the definition of both interstitial and meiofaunal is not very stringent, we here include all the species recorded in the Canary Islands belonging to these groups listed as meiofaunal in the latest published review on meiofaunal annelids (Worsaae et al 2019b). In the Canary Islands, 658 species of non-clitellate annelids ("polychaetes") are known, out of which meiofaunal annelids accounts for 101 species, including those of the last checklist of annelids published for the islands (Núñez et al. 2005), plus a few new species described subsequently (Núñez et al. 2009; Worsaae et al. 2009).

During the workshop, we recorded 36 species of interstitial annelids, 13 of them representing new records for the archipelago (Table 2). These new records include 7 new species, three of them described in this issue (Worsaae et al 2019a, b; Di Domenico et al. 2019). The most diverse family in our samples was Nerillidae with ten recorded species. Amongst them, *Mesonerilla* cf. *luederitzi* was the most common, recorded in five stations, followed by *Nerillidium* sp. and *Mesonerilla armoricana*, both recorded in two marine stations as well as from sediments in Montaña de Arena (Túnel de la Atlántida). *Nerillidium troglochaetoides*, *N. gracile*, and *Trochonerilla* sp. were recorded in single marine localities. In addition, five species of Nerillidae were exclusively found in anchialine localities inside La Corona lava tube: *Meganerilla cesari* and *Mesonerilla runae* only occurred in the sediments of Montaña de Arena; *Mesonerilla xurxoi* and *Leptonerilla diatomeophaga* were found in different cinder patches, being more abundant in Los Jameos del Agua (Worsaae et al. 2009, 2019b); and the stygobitic species *Speleonerilla isa* was exclusively found drifting in the water column in several parts of the flooded lava tube (Worsaae et al 2019a).

Protodrilidae was the second most abundant family in number of species, with nine recorded taxa. In the open ocean, *Claudrilus helgolandicus* (in eight stations) and *Megadrilus schneideri* (three stations) were the most common species, both exhibiting high numbers of individuals. The remaining marine species, i.e. *Lindrilus* sp., *Meiodrilus* sp. 1, *Meiodrilus* sp. 3, and *Protodrilus* cf. *hatscheki*, were recorded in one locality each. The stygobitic protodrilid *Megadrilus pelagicus* was common in the water column of the dark sections of La Corona lava tube, Túnel de la Atlántida and Cueva de los Lagos (Martínez et al. 2017).

Saccocirridae was represented by two species: *Pharyngocirrus* cf. *gabriellae* and *Saccocirrus parvus*, while the remaining interstitial families found in this study had only one species: Polygordiidae, Psammodrilidae, Aeolosomatidae, Diurodrilidae, and Parergodrilidae (Worsaae et al. 2018).

Other interstitial annelids found in our samples were meiobenthic representatives of otherwise macrofaunal families, including two new species of the genus *Macrochaeta* (Acrocirridae), *Raphidrilus nemasoma* (Cirratulidae), *Fauveliopsis glabra* and *F. jameoaquensis* (Fauveliopsidae), *Hesionides arenaria* (Hesionidae), *Questa* cf. *riseri* (Orbiniidae), *Hesionura elongata* (Phyllodocidae), and *Laubierpholoe* sp. and *Pisione guanche* (Sigalionidae). Most of these species already were recorded from the Canary Islands in previous studies (Núñez et al. 1997, 2005, 2009; Martín et al. 1999; Moro et al. 2003; Martínez et al. 2016; Gonzalez et al., 2017, 2018).

In total, 71 species of meiofaunal annelids are known from Lanzarote, and 115 in the Canary Islands, 27 of them are considered endemic (Tables 1 and 2, Supplementary Table 2).

Cnidaria Most meiofaunal Cnidaria belong to the order Actinulida, which includes two exclusively interstitial genera, *Halammohydra* with nine accepted species, and *Otohydra* with one. *Halammohydra* was previously recorded in the sediments of Montaña de Arena (Martínez et al. 2009), although the species was absent in the samples taken during the workshop, as well as in subtidal sediments from Los Abades (Tenerife) (Martínez, unpublished). During our workshop, we found representatives of both genera in Mala. *Halammohydra* was recorded in two stations, from sediments at 11- and 48-m depth; *Otohydra* was recorded only at 11-m depth (Table 2).

In total, two species of meiofaunal cnidarians seem to be present in Lanzarote and the Canary Islands, none of them endemic (Supplementary Table 2).

Gastrotricha Gastrotricha includes, as of May 2019, 855 species, 514 of which are marine and 341 are found in fresh water (Todaro et al., 2019b). Marine species live both intertidally and subtidally, being most abundant in fine- to medium-grained sediments in crystalline waters of coastal areas (e.g. Todaro and Rocha 2004). Selected species have been found in caves or in muddy substrates (Todaro et al. 2006; Sergeeva et al. 2019). Like most other meiobenthic organisms, marine gastrotrichs have a short life cycle and lack larval stages useful for dispersal; consequently, they spend their entire existence within the sediments. Despite these life history traits, many species are not restricted to confined areas; on the contrary, they seem to be widely distributed, with some species being amphi-Atlantic or cosmopolitan (Artois, 2011; Chatterjee et al. 2019).

In the course of the current investigation, gastrotrichs were found at 7 locations and 16 stations along the eastern coast of the island of Lanzarote. Samples yielded 61 species for a total of 96 records. Thirty-six species (27 genera and 11 families) belong to Macrodasyida while 25 species (18 genera, 7 families) to Chaetonotida. Thirty-two are known species while 29 appear to be undescribed taxa or putatively so. Of the 32 known species, two were described from Tenerife and so far appear to be endemic to the Canary Islands, while the other 30 species are also present in other nearby geographic areas, e.g. the Mediterranean Sea and/or the North European coasts. More specifically, 28 species found in Lanzarote are in common with the Mediterranean and 22 are shared with the North European coasts (for detail see Supplementary Table 2 and Todaro et al., 2019a).

Gnathostomulida Gnathostomulida is a group of microscopic, interstitial marine worms with about 100 described species (Sterrer & Sørensen 2015). Previously, five species were

Table 2 Number of species of soft-bodied meiofauna known from the Canary Islands and Lanzarote. "Species Canary Islands" and "Species Lanzarote" summarize both the results in our workshop and species recorded in the literature (see Supplementary Table 2). "Records", "new species", and "doubtful" include only the species found in our survey

	Species Canary Islands	Species Lanzarote	Records	New species	Doubtful
Annelida	115	71	36	11	6
Cnidaria: Actinulida	2	2	2	0	2
Gastrotricha	61	61	61	8	19
Gnathostomulida	6	1	1	0	1
Mollusca: Heterobranchia	4	4	4	3	0
Nemertea	9	6	6*	1	1
Platyhelminthes: Rhabdocoela	79	74	74	29	36
Platyhelminthes: Proseriata	46	39	39	33	4
Priapulida	1	1	1	0	0
Rotifera	15	15	15	0	12
Total	338	274	239	85	81

known from the Canary Islands (Supplementary Table 2), recorded from the islands of Gran Canaria (Playa de las Canteras) and Tenerife (Los Cristianos Bay) in shallow *Cymodocea nodosa* meadows (Sterrer 1997, Riera 2012). During the workshop, individuals of *Austrognathia* were collected in sediments from Montaña de Arena (Túnel de la Atlántida), as well as Mala at the stations at 17 m and 20 m (Table 2). This represents the second record of Gnathostomulida in cave environments, after *Labidognathia longicollis* was recorded from the sediments of a marine cave in Plemmirio (Sicily) (Gąsiorowski et al. 2017). Both records most likely represent marine species that survive in cave interstitial environments rather than a cave exclusive species.

In total, one gnathostomulid species has been recorded in Lanzarote, whereas in total six are now known from the Canary Islands, two of them endemic (Supplementary Table 2).

Heterobranchia, Mollusca Mollusca is a very diverse lineage of animals with 85,000 species. Several lineages traditionally represented amongst the permanent interstitial meiofauna, mostly belonging to Gastropoda (Higgins and Thiel 1988). In this study, we focus on the heterobranchian lineages Acochlidacea and Rhodopemorpha, with 55 described species worldwide (Jörger et al. 2014).

The only Acochlidacea previously recorded in the Canary Islands is *Hedylopsis spiculifera* (recorded as *H. suecica*), found in coarse sand at Los Cancajos beach (La Palma) (Ortea et al. 2009). During our workshop survey, we found another species of acochlidacean, probably representing *Pontohedyle milaschewitchii*, although the specific identification needs to be confirmed with molecular barcoding (Jörger et al. 2012). The species was found in coarse poorly sorted sediments inside La Catedral marine cave. *Pontohedyle milaschewitchii* is widespread in the Mediterranean. In addition to these records, there is an unpublished record for *Hedylopsis spiculifera*, found in subtidal sandy patches at Los Abades, in Tenerife (Martínez and Jörger, unpublished).

We also provide the first record for Rhodopemorpha for the Canary Islands, which we found represented by three different forms, provisionally considered as different species, belonging to

Table 3 Summary of the variables used in the analyses on biological correlates to number of endemic species. The data refers to the species collected during the workshop as well as those previously recorded for the literature in Lanzarote. The count numbers represent the total amount of species that positively score for each biological trait

Group	Median size (mm)	Total	Canarian endemic	New species	Doubtful	Dispersing	Endobenthic	Parthenogenesis
Annelida	4.7	71	20	11	6	42	38	2
Cnidaria	0.5	2	0	0	2	0	2	0
Gastrotricha	0.28	61	10	8	19	0	61	21
Gnathostomulida	1	1	0	0	0	0	1	0
Mollusca	2.55	4	3	3	0	1	4	0
Nemertea	10	6	1	3	1	6	3	0
Rhabdocoela	1.12	74	27	29	36	0	57	0
Proseriata	2.3	39	25	31	4	2	37	0
Priapula	0.95	1	1	0	0	0	1	0
Rotifera	0.25	15	1	1	12	4	0	15

the genus *Helminthope.* They were collected at Punta Jameos and inside Túnel de la Atlántida, both in the water column and at the sediments of Montaña de Arena. The presence of *Helminthope* in the water column suggests that the colonization of Montaña de Arena by interstitial meiofauna might happen after individuals get accidentally dragged inside the cave by tidal currents. During the workshop, five additional specimens of *Helminthope* were collected in littoral coarse sediments at Charca de la Novia (near Orzola) (Norenburg, pers. com.).

In total, four species of heterobranch molluscs are known in Lanzarote, with six species recorded from the Canary Islands, four of them here considered endemic (Supplementary Table 2).

Nemertea Nemertea is a phylum of animals, mostly marine, with ca. 1400 species. Meiofaunal nemerteans are represent by approximately 80 species belonging to several lineages that have colonized the interstitial realm independently. Our samples yielded six species of interstitial meiofaunal nemerteans in Lanzarote corresponding to three morphospecies of *Ototyphlonemertes*, two species of *Cephalothrix*, and one species of *Nemertopsis* (Table 2).

Interstitial nemerteans include a considerable amount of cryptic diversity, with morphologically distinct species complexes including several cryptic species identifiable only by use of molecular data (Leasi and Norenburg 2014). Molecular analyses allowed the identification of *Ototyphlonemertes duplex* D04, *Ototyphlonemertes duplex* D05, and *Ototyphlonemertes santacrucensis* S04 as putative genetic species (Leasi et al. 2016). All individuals of *Cephalothrix* and *Nemertopsis* remain identified to the genus level until molecular analyses are performed.

During the workshop, additional samples collected on the island of La Palma by one of us (JLN) yielded additional individuals of *O. duplex* D04, *O. duplex* D05, *O. duplex* D06, *O. macintoshi* M02, and *O. macintoshi* M03, all putative genetic species.

In total, the number of species of meiofaunal nermerteans known from Lanzarote is now six, with nine species in total recorded from the Canary Islands (Supplementary Table 2). Two species of interstitial nemertean are considered endemic to the archipelago at this time, with *O. duplex* D05 found on both islands, *O. macintoshi* M02 was found only on La Palma. *Ototyphlonemertes santacruzensis* S04 (found only on Lanzarote), *O. duplex* 06 and *O. macintoshi* M03, both found only on La Palma, had close genetic similarity to one or more populations along the coast of mainland Portugal, whereas *O. duplex* D04 had connections to Mediterranean France as well as to the UK and Sweden but, despite extensive sampling, no representation along the Portuguese coast (Leasi et al. 2016, JLN unpublished obs.).

Ototyphlonemertes appear to have very strong prey specificity (as is the case for many hoplonemerteans) as well as granulometry preferences; lack of suitably specific prey and/or habitat could limit potential successful survival in caves (JLN unpublished observations).

Priapulida Priapulid worms (Priapulida) are a small phylum of marine, benthic worms with 22 described species (Schmidt-Rhaesa 2012). Nine species from the genera *Priapulus*, *Priapulopsis*, *Acanthopriapulus*, and *Halicryptus* are macroscopic, whereas the members the remaining genera *Tubiluchus*, *Meiopriapulus*, and *Maccabeus* are meiobenthic. Amongst those meiobenthic genera, *Tubiluchus* is the most diverse with 11 described species worldwide. One single species, *Tubiluchus lemburgi*, was recently described from cave and shallow water sediments in the island of Tenerife (Schmidt-Rhaesa et al. 2013). Additionally, several individuals of that genus were reported from Montaña de Arena, at Túnel de la Atlántida (García-Valdecasas 1985).

During our workshop, *Tubiluchus lemburgi* was collected in Mala, as well as La Catedral marine cave, Cueva de las Gambas, and Montaña de Arena in Túnel de la Atlantida. The sediments where the animals were collected ranged from fine (Mala and Cueva de las Gambas) to poorly or moderately sorted coarse sand (La Catedral marine cave and Montaña de Arena, respectively) (Table 2). The preference of the species of the genus for cave sediments has been previously highlighted, and several species have been described or recorded in cave environments including *Tubiluchus troglodytes* (Grotta Piccola del Ciolo, Lecce), *T. australensis* (unnamed cave in Lizard Island), and *T. corallicola* (Walsingham cave, Bermuda) (Todaro and Shirley 2003). Unidentified *Tubiluchus* larvae were recently recovered from small caves near La Restinga, El Hierro (García-Herrero et al. 2017) (see Sánchez and Martínez, 2019 for a complete review).

Tubiluchus lemburgi is so far the only known meiofaunal priapulid in the Canary Islands and it is considered endemic from the archipelago (Supplementary Table 2).

Proseriata, Platyhelminthes The Proseriata is an order of free-living Platyhelminthes recognizable by their tubiform, plicatus-type pharynx, and usually very elongate, comparatively large body reaching up to 4 mm (Cannon 1986). Proseriates are almost exclusively interstitial and marine, with about 380 species described so far (Tyler 2012). The actual species diversity of the taxon is considered to be largely underestimated (Appeltans et al. 2012), and any sampling campaign reveals previously undescribed species (Curini-Galletti et al. 2012). Only six species were known from the Canary Islands before to this workshop (Supplementary Table 2) (Sopott-Ehlers 1976; Sopott-Ehlers and Ehlers 1980). The high percentage (about 70%) of previously unknown species found in the workshop held at Lanzarote is therefore not entirely unexpected.

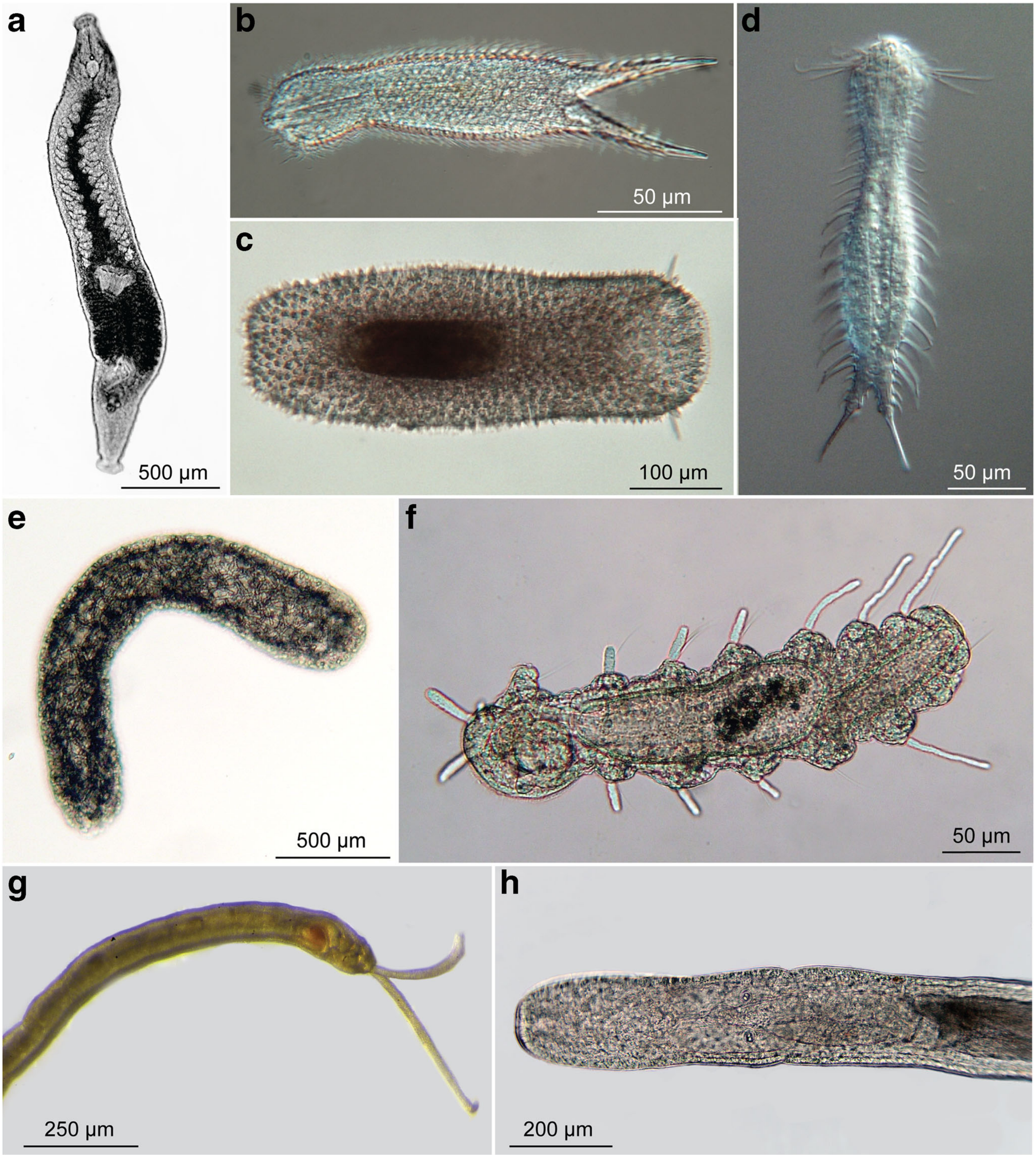

Fig. 2 Light micrographs of different animals collected during the worshop. Proseriate platyhelminth **a** *Paratoplana* sp.; gastrotrichs **b** *Musellifer delamarei*, **c** *Oregodasys cirratus*, and **d** *Chaetonotus lacunosus*; the heterobranch gastropod **e** *Helminthope* sp. 3; the annelid **f** *Trochonerilla* sp., and **g** *Megadrilus schneideri*; the nemertean **h** *Ototyphlonermes duplex*

West African meiofauna is largely unknown: this is certainly the case for Proseriata of which, apart from few data from Boa Vista (Cabo Verde Islands) (Scarpa et al. 2017, 2019a), nothing is known from the entire nearby continental African coastline. The comparatively low number of species shared with other areas of the Atlantic-Mediterranean province is however remarkable: two species with the southern coast of Portugal, seven with western Mediterranean, and only one species (*Otoplana didomenicoi*) shared amongst the three areas (Scarpa et al. 2019a).

On the contrary, the number of species found, although high (39, Table 2), does not particularly differ from other sites where similar workshops have been held, in Mediterranean (Curini-Galletti et al. 2012) and in tropical areas (unpubl. data), also in consideration of the high sampling effort and the diversity of habitats available in Lanzarote. Furthermore, the composition of the local proseriate fauna appears rather unbalanced compared to other parts of the world, as most species diversity is due to a few genera only. Two genera in particular (*Archimonocelis* and *Parotoplana*), out of a total of 17 genera found in the island, accounted for one-third of the total number of species.

A further peculiarity of the proseriate fauna of Lanzarote was the relative rarity of most species, found in single localities, or in very low numbers, and the stark exception represented by the two species of the genus *Archilina*, which in contrast were exceptionally abundant and widespread in most stations, in any kind of substrates and depths (Scarpa et al. 2019b).

In total, 39 species of proseriates are known from Lanzarote and 46 from the Canary Islands, 27 of them being endemic to the archipelago (Supplementary Table 2).

Rhabdocoela, Platyhelminthes Rhabdocoela is a very species-rich taxon of rhabditophoran flatworms, which can be recognized by a true bulbous pharynx and a specific construction of the protonephridial flame cell. Worldwide about 1650 species are described, 60% of which (about 930 species) are from marine or brackish water. Six species of rhabdocoels were previously recorded for the Canary Islands (Supplementary Table 2): *Ceratopera canariensis* and *Diascorhynchu bucina* from sandy beaches in Gran Canaria (Sopott-Ehlers and Ehlers 1980), and *Polycystis naegeli*, *Progyrator mamertinus*, *Graffiellus croceus*, and *Trigonostomum setigerum* from Tenerife (von Graff 1913). These records represent all that was known from the rhabdocoelan fauna of the entire west coast of Africa, highlighting the lack of research in this area. In contrast, about 200 species are known from the Mediterranean (Artois, unpublished data).

During the workshop in Lanzarote, 74 species of rhabdocoels were collected: 28 dalytyphloplanids and 46 kalyptorhynchs. They all belong to the suborder Kalyptorhynchia (Table 2). Amongst them, *Carcharodorhynchus flavidus* was previously known from the Mediterranean (Gulf of Marseille and Sardinia), and North Carolina (USA), and *Gyratrix proavus* from the Baltic Sea, the Northwestern Atlantic Ocean, and the Mediterranean, *Trigonostomum penicillatum* from the Mediterranean and the European and American Atlantic (Willems et al., 2004; Gobert et al., 2019). *Gyratrix hermaphroditus* is a species complex with a worldwide distribution (Artois and Tessens 2008). *Ceratopera sellai* and *Cystirete graeffei* were previously only known from the Mediterranean (Steinböck 1933; Brunet 1965). Three species were described from the material collected during the workshop, but are also known from other areas: *Brunetorhynchus microstylis* also occurs in Southern France, Corsica, Sardinia, and Sweden; *Cheliplana curinii* also occurs in Sardinia; *Proschizorhynchus martinezi* also in Portugal (Gobert et al., 2019); *Typhlopolycystis sarda* also in Sardinia (Schockaert et al., 2019). Eight species described during the workshop can be considered endemic from Lanzarote: *Brunetorhynchus canariensis*, *Carcharodorhynchus worsaae*, *Cheliplana canariensis*, *C. sarniensis*, *Cheliplanilla cavavulcanica*, *C. todaroi*, *Typhlopolycystis pluvialiae*, and *Pseudoschizorhynchoides timoshkini* (Gobert et al. 2019; Schockaert et al., 2019). The five remaining species correspond to four new undescribed species of the genera *Rogneda*, *Paulodora*, *Parachrorhynchus*, *Lagenopolycystis* (Tessens et al. 2014), an unidentified species of the genus *Toia*, and a doubtful species provisionally included in the genus *Proschozorhynchella* (Gobert et al., 2019).

After our workshops, the number of rhabdocoels known in the Canary Islands increased to 80, including 50 kalyptorhynchs and 30 dalytyphloplanids. Fifteen of these species represent so far single island endemic species either from Gran Canaria (2 species) (Sopott-Ehlers 1976) or Lanzarote (13 species) (Tessens et al. 2014; Gobert et al., 2019), while nine are known also from European Atlantic and Mediterranean waters. *Carcharodorhynchus flavidus* might represent a species with amphi-atlantic distribution, although morphological differences found between European, Canarian, and Eastern Atlantic populations might indicate that different disjunct populations actually represent different species within a species complex.

Regarding the diversity of rhabdocoels in subterranean marine and cave environments, the species *Cheliplana sarniensis* was found in a marine cavern in Mala, whereas *Proschizorhynchus martinezi*, *Pseudoschizorhinchus timoshkini*, *Cheliplanilla cavavulcanica*, and *Schizochilus lanzarotensis* have been collected in the sediments of Montaña de Arena in the anchialine cave of Túnel de la Atlántida. The last two species are exclusive from this locality; the rest are found also in open marine sediments.

In total, for Lanzarote, 74 species of meiofaunal rhabdocoels are known in Lanzarote and 80 in the Canary Islands, 59 of them considered endemic (Supplementary Table 2).

Rotifera Rotifera represents a lineage of microscopic aquatic animals with around 2000 described species (Segers 2007). Most rotifers live in freshwater and limno-terrestrial habitats, and only about 400 species have been found in saline waters so far (Fontaneto et al., 2006).

The habitats we sampled in Lanzarote provided 15 species of rotifers based on morphological criteria, four bdelloids and 11 monogononts. Amongst the bdelloids, *Philodina megalotrocha*, *P. roseola*, and *Rotaria rotaria*

Table 4 Biological correlates of diversity in Lanzarote, based on all the soft-bodied meiofaunal species known in the island. Model-averaged parameter estimates are reported. Relative importance for each selected variable is given on a scale from 0 to 1. Predictors with high relative importance values (> 0.75) are highlighted in italics. Abbreviations: p, *p* value; *RI*, relative importance; *std. error*, standard error

	Estimate	std error	RI	*p* value
(Intercept)	− 0.548	0.502	–	0.324
Size	− 0.057	0.093	0.36	0.151
Endobenthic	0.803	0.877	0.15	0.450
Dispersal	− 0.581	0.540	0.20	0.371
Parthenogenetic	*− 2.431*	*1.118*	*0.77*	*0.072*

and an undescribed species of *Rotaria* correspond to new records for Lanzarote. All monogononts were identified to genus level only (Table 2). Amongst them, *Testudinella* sp. does not correspond morphologically to any known species in the genus, while the remaining ten species are considered doubtful. Rotifers notoriously host a large hidden diversity, with several cryptic species for many morphospecies (Gómez et al. 2002; Fontaneto et al. 2011). DNA taxonomy will be necessary to identify some of them and to look for potential cryptic taxa.

Regarding the habitats, seven species were exclusively found in freshwater environments, including Cueva de las Siete Gotas freshwater mine and the freshwater reservoir of Mala. *Philodina roseola* and *Rotaria* sp. were exclusively found in marine environments; *Filinia* sp. and *Lepadella* sp. were found both in marine and in hypersaline habitats associated to saltpans associated to two saltworks: *Testudinella* sp. in Salinas del Janubio and *Proales* sp. 1 in Salinas del Janubio and Salinas del Río.

In total, 15 species of rotifers are now known in Lanzarote, and one of them can be considered as endemic to the island (Supplementary Table 2).

Biological correlates of regional diversity

The factor significantly explaining which taxonomic groups of the meiofauna had higher proportions of endemic species than others in Lanzarote island was reproductive mode (Multimodel Inference: $p = 0.072$, RI = 0.77, Table 4). The proportion of parthenogenetic species was negatively related to the number of endemic species: the groups with a higher proportion of parthenogenetic species (e.g. Gastrotricha, Rotifera) had a lower proportion of endemic species. In fact, none of the parthenogenetic species was endemic from the Canary Islands. The other biological traits revealed low relative importance and no significant effect (Table 4).

Table 5 Ecological correlates of species richness in Lanzarote in the samples collected during the workshop. Species richness is calculated for the total meiofauna as well as for the four groups with more than ten recorded species, and only for the samples where they were present. Abbreviations: *df*, degrees of freedom. Significant predictors are reported in italics

Group	Predictor	df	*F* value	*p* value
Total	Environment	1	2.372	0.133
	Habitat	3	1.365	0.270
	Substrate	3	0.912	0.446
	Residuals	34		
Annelida	*Environment*	*1*	*5.319*	*0.036*
	Habitat	2	0.159	0.854
	Substrate	2	0.204	0.405
	Residuals	19		
Gastrotricha	Environment	1	1.410	0.260
	Habitat	2	0.224	0.803
	Substrate	1	2.633	0.133
	Residuals	11		
Proseriata	Environment	1	0.617	0.441
	Habitat	3	0.807	0.503
	Substrate	3	1.074	0.359
	Residuals	22		
Rhabdocoela	Environment	1	1.318	0.268
	Habitat	3	1.400	0.279
	Substrate	3	1.126	0.304
	Residuals	16		

Environmental correlates of local diversity

Focusing only on the species found during the workshop, for which we had information on the habitat, the overall species richness was not affected by any of the environmental variables (Table 5). Analysing each group separately, significant differences in species richness between marine and anchialine systems were found in Annelida (AnoVA: $p = 0.036$, Table 5), with a higher number of species in the anchialine environments.

The proportion of endemic species was not affected by environmental differences (Table 6). Analysing each taxonomic group separately, only Annelida were significantly affected by the type of environment (anchialine vs marine) (AnoVA: $p = 0.004$; Table 6) and by the type of habitat ($p = 0.008$; Table 6), with a higher proportion of endemic species in anchialine habitats and in caves.

Most of the variability amongst our samples remained unexplained (Adonis: residual $R^2 = 0.756$). Otherwise, differences in species composition were significantly influenced mostly by habitat type (Adonis: $R^2 = 0.103$, $p = 0.001$) (Table 7), and to a lesser extent by substrate ($R^{22} = 0.080$, $p = 0.016$) and environments ($R^2 = 0.060$, $p = 0.042$). Species composition for each

Table 6 Ecological correlates of endemism in Lanzarote in the samples collected during the workshop. Endemism is calculated for the total meiofauna as well as for the four groups with more than ten recorded species, and only for the samples where they were present. Significant predictors are reported in italics

Group	Predictor	df	*F* value	*p* value
Total	Environment	1	1.452	0.237
	Habitat	3	1.946	0.141
	Substrate	3	2.160	0.111
	Residuals	34		
Annelida	*Environment*	1	11.117	*0.004*
	Habitat	3	0.637	0.540
	Substrate	3	6.267	*0.008*
	Residuals	19		
Gastrotricha	Environment	1	0.368	0.557
	Habitat	3	1.700	0.227
	Substrate	3	0.000	1.000
	Residuals	11		
Proseriata	Environment	1	2.410	0.135
	Habitat	3	1.553	0.229
	Substrate	3	1.801	0.189
	Residuals	22		
Rhabdocoela	Environment	1	1.500	0.238
	Habitat	3	1.538	0.244
	Substrate	3	1.696	0.211
	Residuals	16		

Table 7 Ecological correlates of species composition in Lanzarote from the samples collected in the workshop. Species composition is calculated based on the Jaccard similarity index. Significant predictors are reported in italics

Group	Predictor	df	R^2	*p* value
Total	*Environment*	*2*	*0.060*	*0.042*
	Habitat	*4*	*0.103*	*0.005*
	Substrate	*3*	*0.080*	*0.016*
	Residuals	34	0.756	
Annelida	*Environment*	*2*	*0.125*	*0.001*
	Habitat	*2*	*0.096*	*0.021*
	Substrate	*2*	*0.128*	*0.001*
	Residuals	19	0.650	
Gastrotricha	Environment	1	0.070	0.397
	Habitat	2	0.143	0.193
	Substrate	1	0.171	0.185
	Residuals	11	0.720	
Proseriata	Environment	3	0.029	0.695
	Habitat	1	0.128	0.083
	Substrate	2	0.084	0.1073
	Residuals	22	0.758	
Rhabdocoela	*Environment*	*1*	*0.057*	*0.031*
	Habitat	*3*	*0.150*	*0.034*
	Substrate	1	0.044	0.170
	Residuals	20	0.749	

of the groups separately was more affected by type of habitat rather than by any other variable in Rhabdocoela ($R^2 = 0.150$, $p = 0.034$) and Proseriata ($R^2 = 0.128$, $p = 0.083$), and substrate in Gastrotricha ($R^2 = 0.171$, $p = 0.185$), although the results were only significant for Rhabdocoela. The variability in the species composition of Annelida was significantly explained both by the environments ($R^2 = 0.125$, $p = 0.001$) and the substrate ($R^2 = 0.128$, $p = 0.001$) (Table 7). However, as for the total meiofauna, most of the variability in similarity across the samples remained unexplained.

Discussion

Diversity of meiofauna in the Canary Islands

We discovered 239 species during our 2-week inventory. From these, 135 species were new records for the Canary Islands, including 86 new species to science. Our results considerably increase the diversity of most meiofaunal groups known in the Canary Islands (Supplementary Table 2), which were dramatically under-investigated before our workshop. Before this study, only six species of Rhabdocoela and six species of Proseriata were known from the Canary Islands, based on a handful of studies (see references in Gobert et al., 2019). With 74 recognized species of Rhabdocoela and 39 of Proseriata, our study multiplies the diversity of these groups four and seven times respectively. Gastrotricha were slightly better investigated in the Canary Islands, with 10 published records from two studies (Todaro et al. 2003; Rothe and Schmidt-Rhaesa 2010). Yet, out of the 61 species found in our workshop, 35 represent new records and at least 8 new species. Our results increased the diversity even for those groups that have been repeatedly investigated in the Canary Islands, such as annelids (Núñez et al. 2005). From the 36 species of annelids that we found, 13 were new records, accounting for 11 new species.

One might argue that the high proportion of new species is related to the fact that very few studies have been done in the Canary Islands before. However, previous meiofauna surveys performed with a similar sampling intensity in better-studied areas, such as Sweden and Sardinia, also yielded an impressively high number of new records and species (Willems et al. 2009; Curini-Galletti et al. 2012). In Sweden, 154 soft-bodied meiofaunal species were found, including 69 new records for Sweden with 25 new species to science; in Sardinia, 203 species were found, including 76 new species. These findings are relatively similar to those of Lanzarote, despite that comparison between the three surveys is not straightforward. It is difficult to determine whether the observed differences are true or due to different sampling strategies (i.e. investigated taxonomic groups, taxonomic specialist involved, number of stations, diversity of habitats, etc.). The effect of sampling bias and effort is a well-known problem in all biodiversity inventories, even in well-studied groups of organisms (Barbosa et al. 2010; Boakes et al. 2010), and the problem becomes potentially massive for meiofauna (Fontaneto et al. 2012).

While the number of new records and species was similar amongst Sweden, Sardinia, and Lanzarote, the number of indeterminable specimens was higher in Lanzarote. Whereas only 3 species of uncertain identity were found in Sweden, 33 were recorded in Sardinia and 81 in Lanzarote. This high number of doubtful records could be related to the lack of studies in neighbouring areas of Northwest Africa, or to the presence of many morphologically divergent species in the island. In contrast, Sweden and Italy have a long history of taxonomic research on flatworms (Karling 1940; Westblad 1948; Ax 1956a, b; Martens and Curini-Galletti, 1994), meiofaunal annelids (e.g. Pierantoni 1908, Jägersten 1952, Swedmark 1959, Jouin 1970) and rotifers (Ricci and Fontaneto 2003, Fontaneto et al. 2006), so the species found there could more accurately be identified to species level.

The lack of meiofauna studies in Northwest Africa also complicates an evaluation of the biogeographical relationships of the marine meiofauna from the Canary Islands. Mostly based on data on macrofauna, the Canary Islands has been traditionally included within the Atlantic-Mediterranean Marine Province (Bianchi et al. 2012), while more recently, it has been grouped together with Azores, Madeira, and Selvagens as a single marine ecoregion within the Lusitanian province (Spalding et al. 2007). However, due to their geographical position, Canary Islands host a considerable number of West African macrofaunal species (Hernández and Rolán 2011). Future survey in the coast of Northwest Africa might yield several of the meiofaunal species here considered as endemic, thereby changing our picture on the affinities of the Canarian meiofauna. However, with our present knowledge, the peculiarity of the Canarian fauna with respect to the rest of the Atlantic-Mediterranean Province suggests that biogeographical subdivisions based on macrofaunal taxa, mostly with more efficient ways of dispersal, may not apply to meiofaunal taxa.

Effects of biological and environmental variables on diversity

The factor significantly explaining which taxonomic groups had higher proportions of endemic species was the reproductive mode: taxa including more parthenogenetic species had a lower proportion of endemic species. Surprisingly, neither body size nor the presence of dispersal stages, which are known correlates of the possibility for frequent long-distance dispersal (Fenchel and Finlay 2004; Fontaneto 2019), had any significant effect on the number of endemic species. The role of parthenogenesis as a correlate of endemism is difficult to explain. Parthenogenetic species can establish populations starting from a small number of individuals, even only one female, avoiding the energetic costs of sexual reproduction (Tilquin and Kokko 2016). In insular terrestrial fauna, it has been demonstrated that there is a higher proportion of parthenogenetic species than in the nearby continental areas (Cuellar 1977). However, in most of these terrestrial groups, parthenogenesis evolves after the colonization of the insular environments, leading to speciation due to the isolation between insular parthenogenetic and continental sexual populations. In our analyses, we found the opposite effect, with the percentage of parthenogenetic species inversely related to endemism. This is because the parthenogenetic species in our study belong to parthenogenetic lineages (i.e. Rotifera and Gastrotricha) already present outside Lanzarote. Given that, we cannot explain the role of parthenogenesis on endemism with our current data.

Regarding the explanatory effect of environmental variables on differences in richness and percentage of endemic species, we found significant effects of the environment (marine versus anchialine) only on Annelida, which showed more species with a higher percentage of endemic species in anchialine environments. Although the higher richness of annelids in anchialine environments might seem surprising and it might be biased due to the higher effort devoted to the study of annelid diversity in La Corona lava tube, the number of annelids species in La Corona is indeed very high, representing the second group in diversity after crustaceans (Martínez and Gonzalez, 2018). In fact, La Corona lava tube is the cave with the highest number of endemic species of annelids in the world (Gerovasileiou et al. 2016). Part of this high species richness is due to the unusually high diversity of certain families such as Nerillidae, which is represented by six species inside the cave, five of them endemic and often co-occurring in the same samples (Núñez et al. 1997; Worsaae et al. 2009; Worsaae et al 2019a, b). Annelid species richness is high in general in the sediments of Montaña de Arena and Los Jameos del Agua lake (in La Corona lava tube), with a number of marine species present also outside the cave (García-Valdecasas 1985; Núñez et al. 1997; Brito et al. 2009; Martínez et al. 2016). Despite being inside the cave, these sediments resemble marine interstitial environments with comparatively high amounts of trophic resources. While reaching these habitats might be problematic for other meiofaunal groups, the presence of larvae in some species and the ability to glide in the water using the parapodia or the ciliary bands might have favoured the colonization of these environments by the minute annelids from the surrounding non-cave marine sediments possibly travelling underground with the tidal currents. Furthermore, Annelida is also the only soft-bodied meiofaunal group with species that are fully adapted to live in the water column of the cave, with two species exclusively living there (Martínez et al. 2017; Worsaae et al., 2019a). In contrast to annelids, other meiofaunal groups showed no significant differences in richness or endemism between anchialine and marine environments. This might be because many of these meiofaunal groups show lower dispersal abilities than annelids, with many of them lacking a larval dispersal stage, or being interstitial and often provided with adhesive glands and negative phototropism preventing them from emerging outside the sediments. Furthermore, except for annelids, most of the studied species lack appendages or other structures that favour their drifting in the water column, which also might reduce their chances of reaching interstitial environments deep in the cave.

In agreement with our expectations, the largest differences in species composition were found amongst habitats, with type of habitat (i.e. caves, ponds, subtidal environment, and sandy beaches) and of substrates being the most strongly influencing factor on species composition. This result was robust across all groups. The presence of different species assemblages across these different types of habitats is well known across macrofaunal species. Regarding meiofauna, several studies have already shown the presence of specific communities in sandy beaches (Di Domenico et al. 2009) and caves (Todaro et al. 2006; Janssen et al. 2013; Riera et al. 2018), supporting the pattern we could see in Lanzarote.

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Compliance with ethical standards

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

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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