Lanzarote and Chinijo Islands: An Anchialine UNESCO Global Geopark

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Abstract

The Lanzarote and Chinijo Islands UNESCO Global Geopark hosts one of the most extensive and diverse volcanic anchialine ecosystems in the world, consisting of water bodies with marine origin that penetrated inland through coastal crevicular systems. Marine infiltration is facilitated by the low rainfall and the permeability of the coastal terrains. Best known for Túnel de la Atlántida, Lanzarote has other types of anchialine habitats, such as pools, lakes, and even hand-made wells, all of them interconnected with the crevicular system. So far, 39 endemic stygobitic species of crustacean, annelids, and platyhelminthes have been described in the island. Some of them belong to lineages previously interpreted as Tethyan vicariant relicts because they belong in ancient groups restricted to caves situated in areas along the coastline of the ancient Tethys Sea, such as Mexico, Bahamas or Western Australia. Others, instead, have clear affinities with deep-sea lineages, suggesting that their ancestors might have dispersed into the island from surrounding deep-sea environments. In overall, while the anchialine habitats of Lanzarote are relatively small in comparison to other regions, the presence of so many species with such a diverse origin have puzzled zoologists and biogeographers throughout the 20th century, who have regarded the island as a model to understand the origin and evolution of similar groups in other areas of the world. The anchialine habitats in Lanzarote are subject to intense recreational use and the island itself is a major touristic destination. However, geologist and biologist working in the local government offices, as well as in UNESCO Global Geopark and Biosphere Reserve Institutions have started close collaborations with the touristic centers and independent scientist from several universities and research centers around the world with the goal of implementing novel conservation policies based on the results of state-of-art research. This strategy will ensure not only a better understanding of the anchialine ecosystems in the island in the near future, but also its long-term preservation.

Keywords

Anchialine • Stygofauna • Evolutionary biology • Lanzarote • Cave fauna

1 What Anchialine Ecosystems Are?

Anchialine ecosystems consist of tidally influenced subterranean water bodies with marine origin, often located within crevicular and cavernous karst and volcanic terrains, extending inland to the limit of the seawater penetration (Bishop et al. 2015). The term derives from the Greek word *anchialos* or 'near the sea', and it was coined to describe pools with brackish or marine waters hosting assemblages of 'red shrimp' never found elsewhere in marine or freshwater environments (Holthuis 1963). Given their tidal fluctuations, these pools were assumed to have subterranean connections with the surrounding marine and inland waters. After cave diving techniques were revolutionized scientists, investigations in several of these pools showed that they represented entrances to extensive underwater labyrinths, many of which contain both hydrological and faunistic components fitting

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original 'anchialine' definition by Holthuis (Sket and Iliffe 1980; Iliffe et al. 1984b). Despite both geological and geographical differences, cave diving explorations consistently revealed caves with comparable hydrology that hosted assemblages of extraordinary animals. Among these animals, mostly crustaceans, were the new class Remipedia (Yager 1981), the new peracaridan order Mictacea (Bowman et al. 1985), the new copepod order Platicopioida (Fosshagen and Iliffe 1985), as well as several new families, genera, and numerous new species (Fosshagen and Iliffe 1991, 1998; Sterrer and Iliffe 1982; Huys 1996; Huys and Iliffe 1998). Nowadays, anchialine ecosystems are the focus of multidisciplinary integrative research from a variety of scientific fields, including microbiology, ecology, and hydrology (Wicks and Humphreys 2011).

Anchialine systems are more often found in karstic limestone throughout tropical localities and typically contain both freshwater and marine water layers (Brankovits et al. 2017). The most extensive anchialine systems are described from the Yucatán Peninsula (México), being the largest anchialine cave the Sistema Ox Bel Ha (Quintana Roo) with more than 270 km of surveyed passages interconnect with hundreds of entrance pools (Coke 2012). Other geographical areas with large karstic anchialine systems are the Bahamas, Bermuda, and the Balkan Peninsula. Anchialine systems are also present in volcanic terrains although they are less common and mostly restricted to island locations, such as the Canary Islands, Galapagos, Ascension, Hawaii, and Iceland (Iliffe and Kornicker 2009). Anchialine habitats in these locations are found in the form of lava tubes, tectonic faults, and lava rock pools (Iliffe 1992). Lava tubes are the most extensive of these three forms, and they are originated during eruptions of fluid basaltic lava in which the slow-moving surface is cooled forming a drain that favors the progression of the lava flow inside for distances ranging from few meters to several kilometers. Once the eruption ceases, the hollow drain becomes the lava tube (Dragoni et al. 1995). Typically, lava tubes are formed above the sea level, flowing towards lower elevations until the lava reaches the coastline and is suddenly cooled by the surrounding marine waters, preventing the tube from progressing any further. The longest anchialine lava tubes of the world are located in the Canary Islands, but they have also been reported in Hawaii and Galapagos archipelagos (Kensley and Williams 1986; Figueroa and Hoefel 2008; Martínez et al. 2016). Anchialine volcanic tectonic faults are better described in the Galapagos, where they are known as 'grietas' or faults (Iliffe 1992). These faults are formed when a crustal block moves up or down with respect to a neighbor along a nearly vertical fracture, producing series of high cliffs and deep fissures (Simkin 1984). Those fissures close to the coastline may extend below the sea level and contain anchialine pools. Finally, lava rock pools occur in low-lying terrain near the coastline, where highly uneven and irregular lava flows have left behind low spots, cracks or gas pockets that extend below the sea level. Anchialine lava pools are an iconic anchialine habitat in the Hawaiian archipelago (Brock and Bailey-Brock 1998).

2 Lanzarote and Chinijo Islands: An Anchialine UNESCO Global Geopark

Lanzarote harbors the most extensive anchialine ecosystem in the Eastern Atlantic and one of the most extensive volcanic anchialine habitats in the world. The presence of this ecosystem in Lanzarote is a consequence of the marine infiltration through the coastline, which is favored by the low annual rainfall as well as the high permeability of the volcanic materials along the coastline. These two features are intimately related to the geological history of the island (Martínez et al. 2016) (Fig. 1).

The arid climate of Lanzarote is favored by its low altitude. The highest mountains of the island are Los Ajaches and Famara massifs, which today consist of dry and highly eroded ridges reaching 560 and 671 m high respectively. However, they looked very differently during their infancy, 14.5–3.8 years ago, when geologist think that they were higher than 4000 m and capable to collect the moisture carried by the trade winds (Carracedo and Badiola 1993). The precipitation resulting from this moisture facilitated the growth of laurel forests, and also infiltrated the volcanic rocks forming a relatively shallow aquifer, thicker in the interior of the island and tapering towards the coastline. However, as erosional processes reduced Los Ajaches and Famara massifs, they progressively lost their capability to capture of trade-wind precipitation. Eventually, the mountains laid below the trade-winds moist layer, bringing as a consequence a dramatic reduction of the rainfall and the aridification of the island (Machín and Pérez-Torrado 2005). The dry climate favored the overall shrinking of the freshwater aquifer, which was progressively replaced by marine waters infiltrated through the coastline (Custodio 1992).

The permeability of the volcanic materials in the coastal lowlands depends on the presence of porous volcanic rocks, as well as crevices and lava tubes, which produce a network of interconnected void spaces that can be occupied by the infiltrating marine waters. The precise extension and distribution of this crevicular system in Lanzarote remains unknown, but it is most likely non-homogeneous and concentrated in certain areas along the coastline depending on the nature and composition of the volcanic terrains, which varied during different eruptions and across different areas (Carracedo and Badiola 1993). Most anchialine habitats in Lanzarote are known from Malpaís de la Corona (Fig. 2a), a stark, jagged lava field on the northern tip of the island originated from eruptions of La

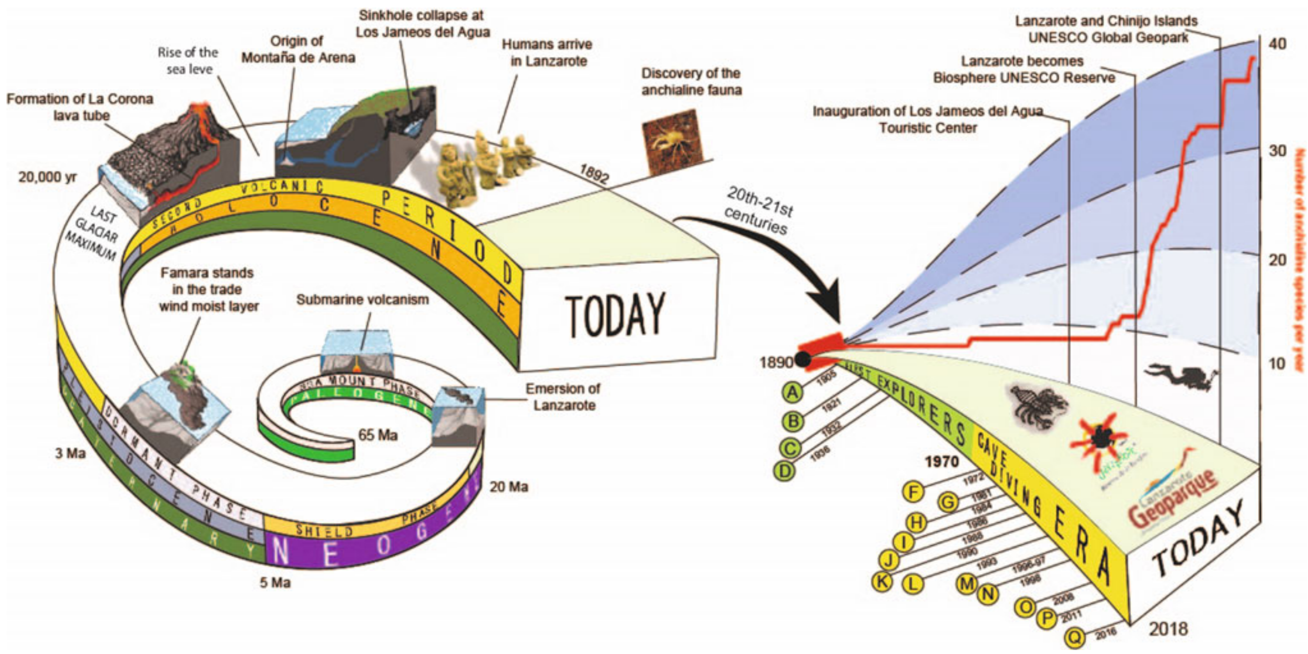

Fig. 1 Timeline showing the major events on the history of Lanzarote and its anchialine ecosystems. The main events are highlighted on both timelines, corresponding the whole geological history of the islands (left) and the 20th and 21st centuries (right). A. Studies of the morphology of *Munidopsis polymorpha* by Calman. B. Studies on the anatomy of the reduced eyes of *Munidopsis polymorpha* by Harms. C. Description of mysid crustacean *Heteromysoides cotti*. D. Monograph of the ecology of Los Jameos del Agua lake by Fage and Monod. F. First dive in Túnel de la Atlántida by Hermanos Guerra. G. Italian "Mondo Somerso" and Spanish 1st STD Expeditions. H. Description of remipede *Morlockia ondinae*, and first ecological studies at Montaña de Arena. I. The GLPS/FFS-SCB Expedition reaches the end of Túnel de la Atlántida, studies in wells by Wilkens and collaborators. J. Revista GEO Cave Diving Expedition reaches the end of Túnel de la Atlántida, first studies in Montaña Bermeja anchialine pools. K. Ecological studies on the biology of *Munidopsis polymorpha*. L. Discovery of Charcos de Luis in Caletón Blanco. M. Discovery of the interstitial fauna at Los Jameos del Agua. N. Discovery of several cave copepods. O. Atlantida Cave Diving Expedition and Discovery of *Morlockia atlantida* and *Meganerilla cesari*. P. 1st International Workshop to Cave and Anchialine Meiofauna and discovery of *Megadrilus pelagicus*

Corona Volcano. The low altitude and the high permeability of the volcanic materials in this area favors marine infiltration at least 500 m inland. The most remarkable geological feature of the Malpaís de la Corona is La Corona lava tube, which traverses the lava field over 6.2 km in southeasterly direction, continuing for an additional 1.6 km into the Atlantic Ocean beyond the present coastline of the island, and ending at a maximum depth of 64 m (Carracedo et al. 2003). The cave was primarily formed from the eruption of a lateral vent off La Corona Volcano, although the complex morphology of the cave and the presence of upper and lower sections suggests that several volcanic episodes were involved during speleogenesis (Jantschke et al. 1994). Age estimates based on potassium-argon radiometric methods dated the formation of La Corona lava tube to the last glacial maximum (21,000 ± 6500 years), when the sea level was approximately 50–100 m lower than today (Church et al. 2001). These estimates suggest that the lava tube was formed under subaerial conditions across La Corona lava field until the lava flow was abruptly stopped by the sudden cooling consequence of its contact with the Atlantic Ocean. Flooding of La Corona lava tube occurred more recently, after the last glacial maxima, when the sea level rose to its present position (Carracedo et al. 2003) (Fig. 2e).

La Corona lava tube is divided into several sections by secondary collapses or 'jameos', although only three of them lead to anchialine section (Carracedo et al. 2003). The most inland of these sections is known as Cueva de Los Lagos, which consists of a sinkhole opening 600 m from the coastline and leading to a partially flooded passageway that ends in a short sump (Martínez et al. 2016). Downstream, this sump is separated by an artificial collapse from the second section, known as Los Jameos del Agua, which includes a partially illuminated, tidal lake integrated into a tourist center (Wilkens and Parzefall 1974) (Fig. 2f, g). The third anchialine section, known as Túnel de la Atlántida, is also accessed from a pool in the touristic center, from which a 1.6 km-long, completely submerge passageway extends under the seafloor without any conspicuous connection to the overlying ocean. Túnel de la Atlántida ends abruptly at a maximum depth of 64 m and it represents the longest flooded lava tube in the world.

Other geological features that allow human access to the anchialine subterranean waters are the so-called anchialine

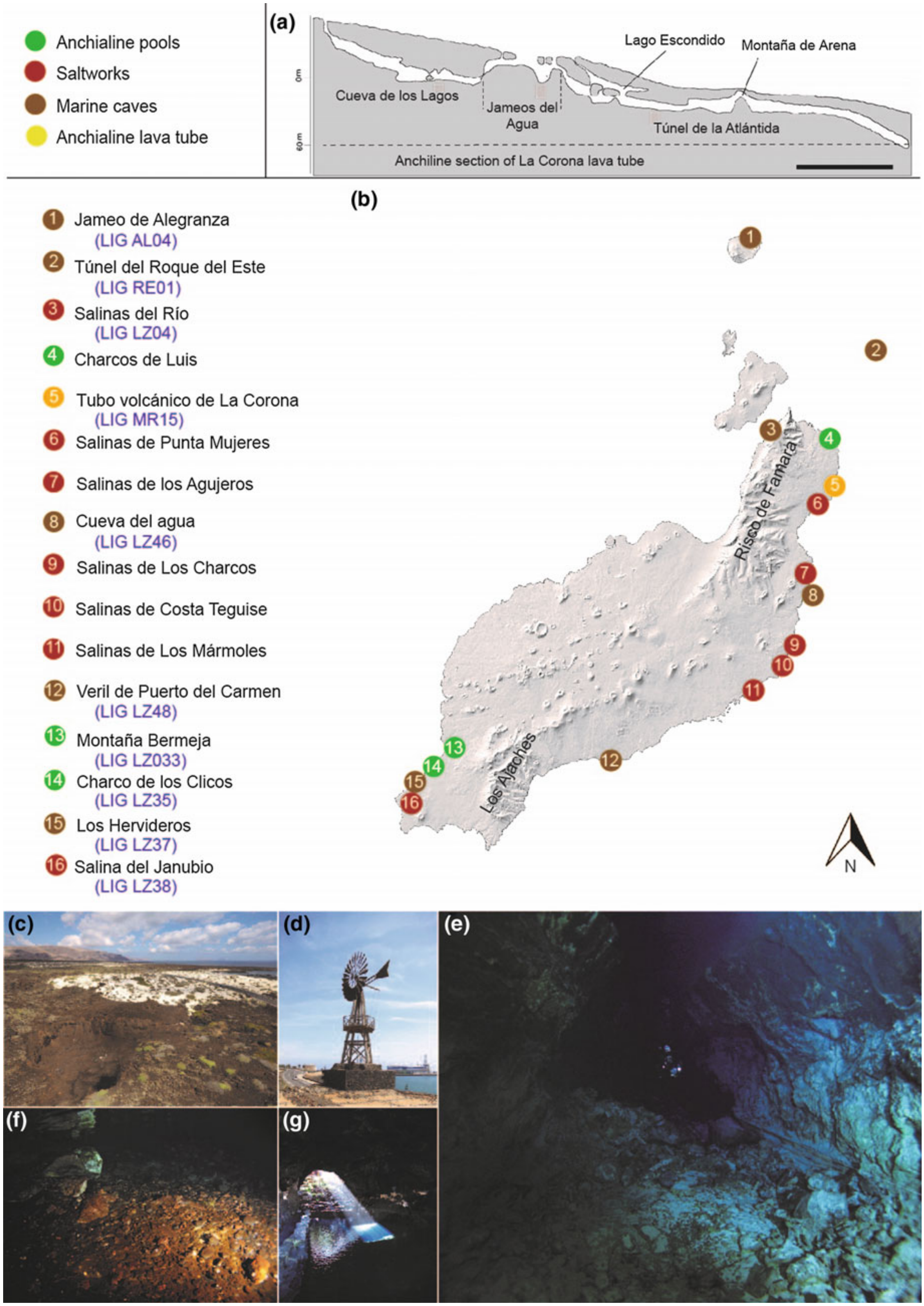

Fig. 2 Anchialine and marine subterranean localities known in Lanzarote. **a** Profile schematic representation of the anchialine sections of La Corona lava tube. The vertical axis is not scaled in relation to the horizontal one. **b** Distribution of anchialine and marine caves, wells and pools in Lanzarote and the Chinijo Islands. The numbers refer to the localities listed on the left. The colours indicated different types of habitats. **c** Aerial view of Charcos de Luis. **d** Abandoned anchialine well in Puerto de los Mármoles. **e** Cave diver hovering in Túnel de la Atlántida, ca. 250 m from the entrance. **f** Underwater image of Los Jameos del Agua lake, showing the brown carpet of benthic diatoms and high densities of *Munidopsis polymorpha*. **g** Los Jameos del Agua lake photographed early in the morning, when sunlight beams illuminate the Western part of the lake

pools. They consist of small depressions that extend beyond the level of the subterranean anchialine waters exposing a comparatively small water body to the surface. The pools are indirectly connected to the sea thorough crevices and fluctuate with the tides. Main anchialine pools in Lanzarote are Charcos de Luis, near Caletón Blanco, and Montaña Bermeja pools, near Los Hervideros (Huys 1988; Wilkens et al. 1993). They both consist of comparatively small, rocky depressions situated near abandoned cinder mines, and therefore it is not currently known if they are natural or manmade. The lagoon at the beach in El Golfo, known as Charco de los Clicos, could represent an additional anchialine habitat. However, this hypersaline lake shows minimal tidal fluctuations and its water composition differs substantially from that of the ocean. The high concentrations of microscopic algae, mainly diatoms and dinoflagellates, give the Charco de los Clicos an intense green color (Luque and Medina 1997).

A third type of anchialine environment in Lanzarote is represented by manmade wells, which were hand dug between the 15th and 19th centuries along the coastline of the island in order to pump subterranean waters into saltpans for salt production (Luengo 1994). Most of these wells are relatively small, ranging between 2–3 m in diameter and averaging 10 m in depth. Since construction, many of these wells have been destroyed, and those that remain are mostly abandoned. Active wells can be found in Salinas del Janubio, Salinas de El Río, as well as around the towns of Costa Teguise, Guatiza, Los Cocoteros (Fig. 2d), and Punta Mujeres (Wilkens et al. 1986).

3 The Life Hidden Amongst the Lavas: A Story of Discoveries

There are 39 stygobitic species (aquatic cave specialists) in Lanzarote, including 27 crustaceans, 11 annelids, and two flatworms (Martínez and Gonzalez 2018) (Fig. 3).

Twenty-eight of them are restricted to the flooded sections of La Corona lava tube, whereas the remaining 12 occur in anchialine wells or pools. Non-stygobitic, marine species are found in certain anchialine ecosystems, being more common in anchialine pools and Los Jameos del Agua anchialine lake, where the presence of light and higher trophic resources facilitate their settlement (Martínez et al. 2009). The main most relevant anchialine environments known in Lanzarote are summarized in Table 1.

3.1 First Discoveries: The Fauna of Los Jameos Anchialine Lake

The earliest discoveries of anchialine endemic species in Lanzarote were made by European researchers who investigated Los Jameos del Agua during short visits (Martínez et al. 2016). The first stygobite discovered by the European scientist was the squat lobster *Munidopsis polymorpha* (Fig. 3 k). However, these lobsters were known long before by the inhabitants of the north of Lanzarote, who called them 'grillos blancos' (white crickets) (Fig. 1). Today, *Munidopsis polymorpha* is very popular amongst locals and tourists and it has been chosen as the animal symbol of the island under the vernacular name of 'jameíto' in reference to the high densities that it exhibits in Los Jameos del Agua lake. *Munidopsis polymorpha* was formally described by zoologist Karl Koelbel from the Natural History Museum of Vienna (Austria) in 1892 from samples collected by Oskar Simony (Koelbel 1892). During his early description, Koelbel already highlighted the remarkable adaptations of *Munidopsis polymorpha* to the darkness of the cave and its similarity with certain deep-sea forms. This resemblance was studied in higher details by zoologists Jürgen Harms (University of Marburg, Germany) and William Calman (University College of Dundee, Scotland) (Calman 1904; von Harms 1921). This last author also described the crustacean mysid *Heteromysoides cotti* (Fig. 3h), named British explorer and zoologist Hugh Cott who collected the types series (Calman 1932). Observations from these works were summarized together with an ecological description of Los Jameos del Agua lake in a monograph published in 1936 by zoologists Louis Fage and Théodore Monod from the Muséum National d'Histoire Naturelle de Paris (Fage and Monod 1936).

The discoveries continued in the late 1960s with the contributions by German zoologists Horst Wilkens and Jakob Parzefall (University of Hamburg). Although most of their research focused on the biology and behavior of *Munidopsis polymorpha* and the ecology of Los Jameos del Agua lake (Wilkens 1970; Wilkens and Parzefall 1974; Parzefall and Wilkens 1975; Wilkens et al. 1990), they also discovered several new cave species as a result of their sampling effort. Their discoveries include isopod *Curassanthura canariensis*, ostracod *Humphreysella wilkensi*, copepod *Neoechinophora karaytugi*, and scale worm *Gesiella jameensis* (Hartmann 1985; Pettibone 1985; Wägele 1985; Huys 1996). Our knowledge on the fauna of Los Jameos del Agua was completed by Spanish zoologist Jorge Núñez and his team (Universidad de La Laguna), who discovered the annelids *Fauveliopsis jameoaquensis*, *Leptonerilla diatomeophaga*, *Macrochaeta* n. sp. and *Mesonerilla* n. sp. in the cinder deposits of the lake (Núñez et al. 1997).

Los Jameos del Agua lake (Fig. 2g) is the only anchialine section in La Corona lava tube that receives sunlight indirectly. The light intensity varies across the lake and during different day hours, but still ensures primary production by pelagic microscopic algae and a dense bed of benthic diatoms (Brito et al. 2009). This primary production sustains comparatively dense populations of animals and allows the coexistence of stygobitic species and typically marine forms

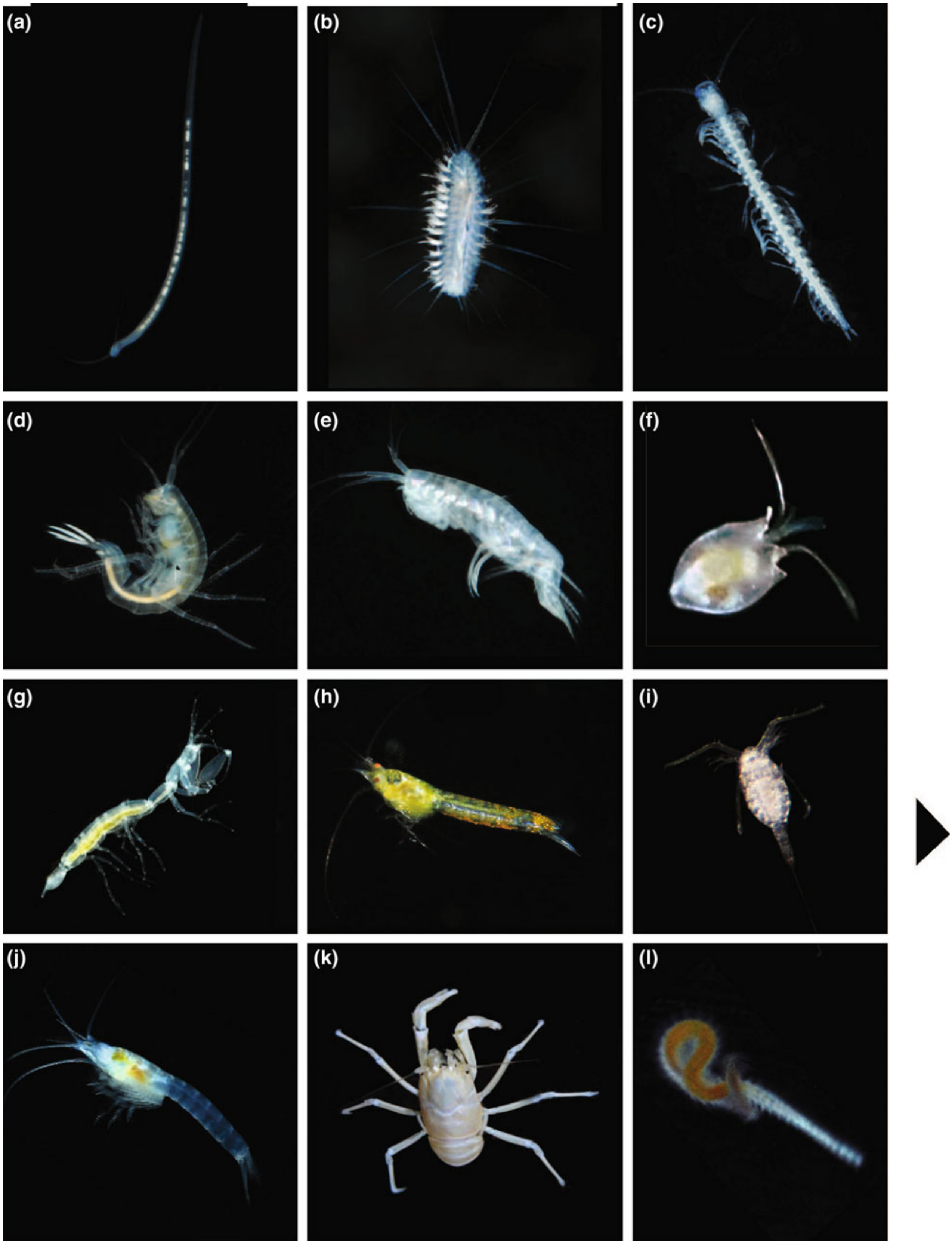

Fig. 3 Stygobitic animals inhabiting La Corona lava tube. **a** Protodrilid annelid *Megadrilus pelagicus*. **b** Scale worm annelid *Gesiella jameensis*. **c** Remipede *Morlockia ondinae*. **d** Amphipod crustacean *Hadzia acutus*. **e** Amphipod crustacean *Spelaeonicippe buchi*. **f** Ostracod crustacean *Humphreysella* sp. **g** Isopod crustacean *Curassanthura canariensis*. **h** Mysid crustacean *Heteromysoides cotti*. **i** Copepod crustacean *Palpophria aestheta*. **j** Undescribed mysid crustacean *Burrimysis* n. sp. **k** Squat lobster *Munidopsis polymorpha*. **l** Undescribed annelid spionid *Prionospio* n. sp

Table 1 Summary of the most important localities regarding the presence of anchialine and marine subterranean fauna in Lanzarote

Anchialine/marine sites	Geosite	Geopark code	Category	Stygobitic species
Famara freshwater mines	Valles colgados de Famara	Lz07	Freshwater mines	–
Charco de los Clicos	El Golfo	Lz35	Lagoon, maybe anchialine	–
Charcos de Montana Bermeja	–	–	Anchialine pool	3
marine caves at Los Hervideros	Los Hervideros	Lz37	Marine cave	–
Tunel de la Atlantida	Tubo volcanico de la Corona—Tunel de la Atlantida	Lz06	Flood anchialine lava tube	33
Jameos del Agua	Tubo volcanico de la Corona—Tunel de la Atlantida	Lz06	Lake in anchialine lava tube	13
Cueva de los Lagos	Tubo volcanico de la Corona—Tunel de la Atlantida	Lz06	Partially flood anchialine lava tube	16
Charcos de Luis	Caleton Blanco	MR04	Anchialine pool	3
Salinas del Rio	Salinas del Rio	Lz04	Wells	–
Jameo de Alegranza	Jameo de Alegranza	AL04	Marine cave	–
Tunel del Roque del Este	Tunel del Roque del Este	RE01	Marine cave	–
La Catedral	Veril de Puerto del Carmen	Lz47	Marine cave	–
Cueva de las Gambas	Veril de Puerto del Carmen	Lz47	Marine cave	–
Cueva del Agua	Cueva del Agua	Lz46	Marine cave	–
marine caves	Charco del Palo—Puerto Moro	Lz45	Marine cave	–
Salinas de Janubia	Salinas de Janubia	Lz38	Wells	–
Salinas de los Agujeros (Los Cocoteros)	–	–	Wells	2
Salinas de los Mármoles	–	–	Wells	3
Salinas de Costa Teguise	–	–	Wells	–
Salinas de Punta Mujeres	–	–	Wells	2
Salinas de los Charcos (Guatiza)	–	–	Wells	–

The name of the geosite that hosts them is indicated when applicable, along with the type of habitat and the number of stygobitic species known in each place

that otherwise cannot survive in the dark sections of the cave (Wilkens and Parzefall 1974; Martínez et al. 2009). Dense populations of mysids, copepods, and ostracods swim in the water column, while the macroscopic benthic communities are dominated by the stygobitic squat lobster *Munidopsis polymorpha* and the peanut worm *Bonellia viridis* (Wilkens and Parzefall 1974; Wilkens et al. 1990; Brito et al. 2009). These large animals feed on the microscopic communities that colonized the spaces amongst the cinders, and include diatoms, dinoflagellates, annelids, and crustaceans (Núñez et al. 1997; Worsaae et al. 2009).

3.2 The Era of Cave Diving: Túnel de la Atlantida

The first dive in Túnel de la Atlántida was performed by the Hermanos Guerra in 1972, who penetrated the first 370 m of the cave using regular open water diving equipment (Oromí and Martín 1990). However, it was during the 1980s when the development of cave diving techniques motivated several international teams to compete to discover the end of the lava tube (Lainez and Pérez-Rijo 1999). The first of these teams integrated the Italian "Mondo Somerso" Expedition, reaching 518 m of penetration in February 1981. They were soon followed by the First Spanish STD Expedition, which explored 861 m in August of that year, discovering Montaña de Arena (see below). Divers from the USA pushed these marks in 1983, when an expedition led by cave diver Sheck Exley reached 1377 and 53 m depth (Exley 1983). A new record was stablished soon after in 1983 by the Second Spanish STD Expedition, whose divers explored 1570 m and stopped only 30 m from the end of the cave due to technical problems. The Second STD Expedition provided the first monograph on the fauna of the cave, and described in detail the so-called Montaña de Arena, a 30 m high sand dune formed approximately 750 m from the entrance by sediments entering the cave through a non-visible crack in the ceiling (García-Valdecasas 1985). The end of the cave at 1618 m was reached in 1986 by the GLPS and FFS-SCB cave diving teams with Belgian and French members (Isler 1987). This record was also equaled by the Spanish GEO Expedition in 1987 (Molinero 1988).

Although the main focus of these expeditions was the exploration of the cave, they brought along fascinating zoological discoveries. The most impressive amongst them was the remipede *Morlockia ondinae* (Fig. 3c), first discovered by bioespeleologist Thomas M. Iliffe in 1983 (Texas A&M University) (Iliffe et al. 1984b), but described by zoologist Antonio García-Valdecasas in 1984 (Museo Nacional de Ciencias Naturales de Madrid) (Garcia-Valdecasas 1984). These and subsequent diving expeditions mainly organized by Iliffe yielded the discovery of additional stygobitic animals including the annelid *Speleobregma lanzaroteum*, thermosbaenacean *Halosbaena fortunata*, ostracods *Humphreysella phalanx* and *Eupolycope pnyx*, and copepod *Enantronia canariensis* (Bertelsen 1983; Bowman and Iliffe 1986; Kornicker and Iliffe 1995; Jaume and Boxshall 1997; Jaume et al. 1999; Koenemann et al. 2009).

These discoveries motivated new expeditions between 2008 and 2017 with the aim to better investigate the fauna of the cave. The main of those were the 2008 Atlantida Cave Diving Expedition led by Prof. Thomas M. Iliffe, and the 1st-international Workshop to Anchialine and Marine Meiofauna 2011 organized by Alejandro Martínez and Katrine Worsaae (University of Copenhagen, Denmark). The surveys of the water column done during these two expeditions led to the description of the new remipede *Morlockia atlantida* (Koenemann et al. 2009), and the annelids *Megadrilus pelagicus* and *Speleonerilla isa* (Martínez et al. 2017; Worsaae et al. in press); as well as the first genetic analyses of annelids *Speleobregma lanzaroteum* and *Gesiella jameensis* (Fig. 3b) (Martínez et al. 2013; Gonzalez et al. 2018a). These expeditions also focused on the fauna at the sediments of Montaña de Arena, leading to the discovered of new species of annelids, crustaceans, and flatworms (Núñez et al. 2009; Worsaae et al. 2009; Gobert et al. 2017).

The total darkness of Túnel de la Atlántida favors the presence of stable water temperature (ca. 18 °C) and lower dissolved oxygen (ca. 3.7–5.7 mg/L) compared to the surrounding ocean (Wilkens et al. 2009). Contrary to other anchialine caves, the water column in Túnel de la Atlántida is poorly stratified, fully marine, and affected by minimal currents due to tidal exchange (Jantschke et al. 1994). These currents produce small fluctuations of the oceanographical parameters with slightly lower salinities and higher oxygen during the low tide (Wilkens et al. 2009). The lack of sunlight prevents photosynthetic activity, and the cave ecosystems is sustained by the particulate organic material introduced through tidal exchange or infiltration across the overlying lava rock (Iliffe et al. 2000; Wilkens et al. 2009). It remains unknown if chemoautotrophic production from low concentrations of dissolved inorganic compounds occur within the dark remote sections of La Corona lava tube, as it has been described in other anchialine systems in the Caribbean (Pohlman 2011; Brankovits et al. 2017). Since particulate organic matter is mostly found in the water column, most of the stygobites are suspension feeding crustaceans (Fig. 3d–f, i, j) or annelids capable of collecting small food particles while swimming (Iliffe et al. 2000). These suspension feeders serve as preys to the remipedes *Morlockia ondinae* and *Morlockia atlantida*, the scale worm *Gesiella jameensis*, and the copepod *Enantronia canariensis*. While remipedes and copepods capture the preys with specialized raptor appendages, *Gesiella jameensis* uses a protruding proboscis armed with two pairs of jaws (Koenemann et al. 2007; Gonzalez et al. 2018b). The claws of the remipedes are connected to venomous glands capable of producing a lethal cocktail of peptidases and putative neurotoxic proteins (von Reumont et al. 2017).

The benthic environments in Túnel de la Atlántida mostly include rock surfaces and patches of lava debris distributed throughout the lava tube (Martínez et al. 2009). These patches superficially resemble interstitial environments but exhibit similar permeability to that found at the surrounding subterranean crevicular environment. Therefore, they do not harbor typical interstitial species but rather a few stygobites in low abundances. The only exception is the dimly illuminate debris near the entrance of the cave, where a comparatively high number of species can be found (Fig. 2f) (Martínez et al. 2016). True interstitial environments are characterized by smaller sized sediment particles, which in La Corona are restricted to Montaña de Arena. The spaces amongst the sediments of the dune harbor a rich fauna which includes typical interstitial groups such as annelids, platyhelminths, gastrotrichs, gnathostomulids, priapulids, and crustaceans (García-Valdecasas 1985; Núñez et al. 2009; Worsaae et al. 2009; Gobert et al. 2017).

3.3 Windows to the Underworld: Anchialine Pools and Wells

Anchialine pools and wells in Lanzarote were mainly investigated by two teams: one led by Prof. Jan Stock from the Zoological Museum of Amsterdam (the Netherlands) and the other by Prof. Horst Wilkens from the University of Hamburg (Germany). Both teams mainly focused on crustaceans, and while some of the species they discovered were new to science, such as the copepods *Boxshallia bulbantenulata* and *Stephos canariensis* (Huys 1988; Boxshall et al. 1990); others were already known from La Corona lava tube (Wilkens et al. 1986). The presence of the same species in La Corona lava tube and comparatively distant wells or pools provided first indirect evidence for connectivity among the island's anchialine habitats and laid the foundation for later theories of dispersal between distant caves through the crevicular systems (Wilkens et al. 1986, 1993; Rondé-Broekhuizen and Stock 1987; Sánchez 1991).

Anchialine pools (Fig. 2c) are interesting from an ecological point of view because they harbor particular assemblages of animals, which combine both marine and stygobitic species. These assemblages are dominated by the amphipod *Parhyale multispinosa*, which should be considered as a 'pond specialist' capable of coping with extreme changes in both temperature and salinity while forming permanent populations in the pools (Martínez et al. 2016). True stygobites, such as *Munidopsis polymorpha* (Fig. 3k) and *Burrimysis sp*. (Fig. 3j), are found in some pools specially during nighttime, when they can feed on decomposing organic matter, green algae, and cyanobacteria avoiding the higher temperatures and risk of predation brought by the daylight (Wilkens et al. 1993). The abundant resources in the pools also facilitate the presence of marine intertidal species, including blenny fish, sea stars, crabs, and shrimp. Interestingly, the endangered European eel *Anguilla anguilla* has been spotted several times in Charcos de Luis, at the northern tip of Lanzarote, probably entering the pools from the ocean through subterranean crevices (Wilkens et al. 1993; Martínez and Gonzalez 2018).

Anchialine wells (Fig. 3d) ecologically differ from pools mainly because they are lined by steep walls, which protect the limited water from direct sunlight and the daily extreme temperatures. The bottoms of these wells mostly consist of gravel and mud, but natural or anthropogenic debris is often present. Few stygobites have been found in wells, including the amphipod *Hadzia acutus*, ostracod *Humphreysella wilkensi*, mysid *Heteromysoides cotti*, thermosbaenacean *Halosbaena fortunata*, and squat lobster *Munidopsis polymorpha* (Martínez and Gonzalez 2018). However, while Hadzia acutus has been found among the debris in the bottom of the wells, all the remaining species have only been collected with baited traps, suggesting that they might live in the surrounding crevices and migrate into the wells attracted by the bait (Wilkens et al. 1986).

3.4 Exploration of Marine Littoral Caves

Marine caves differ from anchialine caves in having a direct connection with the surrounding ocean, large enough to allow the passage of a diver. Several marine caves in Lanzarote are important from the geological point of view and included amongst the geosites of the Lanzarote and Chinijo Islands UNESCO Global Geopark (Table 1). Ecologically, marine caves can be regarded as ecotones between marine open to subterranean environments representing natural gradients with decreasing incidence of light and presence particulate organic matter from the entrance to the bottom (Gili et al. 1986). This gradient favors the presence of different communities of organisms with typical marine species near the entrance and an increasing amount of cave specialists towards the bottom. Within the Canary Islands, the marine caves in Lanzarote are poorly known compared to those in Gran Canaria, Tenerife, and La Palma (Álvarez et al. 2005; Sangil 2007; Riera et al. 2018), where preliminary research have highlighted the existence of specific communities of the organisms on the walls (Cruz 2002; Martínez et al. 2004; Álvarez et al. 2005), and the sediments (Corberá et al. 2001; Herrera et al. 2016, 2017; Riera et al. 2018), with an increasing number of new species of crustaceans, flatworms, annelids, and kinorhynchs (Riera et al. 2007; Martínez et al. 2013; García-Herrero et al. 2017; Gobert et al. 2017). Since marine caves are directly connected to the ocean, the presence of specific assemblages and cave exclusive species is more likely related to the particular ecological conditions inside the caves, rather than to physical isolation.

4 Geological Evolution of Lanzarote and Their Effect on the Endemic Cave Fauna

The anchialine ecosystems of Lanzarote are inhabited by strange creatures, most of them representing unique animal lineages never found in the sea. How these animals arrived and evolved in Lanzarote remains as an open question, which we cannot answer without considering the geological evolution of the island. Many of these stygobitic lineages belong in genera, families, orders or even classes that are restricted to anchialine caves spread thorough broad geographic ranges including Australia, the Caribbean, and the Indopacific (Wilkens et al. 2009). Such disjunct global distribution pattern is shared by different animal groups such as remipedes, thermosbaenaceans, thaumatocyprid ostracods, and spionid annelids (Martínez and Gonzalez 2018). This so-called full Tethyan distribution pattern has been traditionally interpreted as the result of cave colonization by marine shallow water species along the coasts of the Tethys Sea during the Mesozoic, followed by vicariant events driven by plate tectonic and changes in the sea level (Stock 1993; Juan et al. 2010). However, since Lanzarote is only 14.5 Ma and it has never been connected to the coasts of the Tethys (Hou and Li 2018), the discovery in the island of several of these stygobites challenged vicariant theories and drove the search for explanations that include some form of dispersal.

As an alternative, many of the stygobites found in Lanzarote present a clear affinity with groups of animals otherwise exclusively found in the deep-sea (Iliffe et al. 1984b). This includes the annelids *Speleobregma lanzaroteum*, *Fauveliopsis jameoaquensis*, and *Gesiella jameensis*, the squat lobster *Munidopsis polymorpha*, the thaumatocyprid ostracods *Humphreysella wilkensi* and *H. phalanx*, and several species of misophrioid copepods (Kornicker and Sohn 1976; Bertelsen 1983; Pettibone 1985; Ohtsuka et al. 1993; Boxshall and Jaume 1999; Núñez et al. 1997). A deep-sea affinity not necessarily implies deep-sea origin (Boxshall and Jaume 1999; Jaume et al. 2000; Martínez et al. 2013), but phylogenetic analyses have indicated that at least the ancestors for the cave lineages containing the scale worm *Gesiella jameensis* and the squat lobster *Munidopsis polymorpha* originated in the deep sea (Ahyong et al. 2011; Gonzalez et al. 2018a). The details on how the hypothetical deep-sea ancestors of these species reach the island remains speculative. One possibility is that they arrived during the seamount stage, when submarine volcanic activity might have produced vent-like habitats resembling those currently occupied by the deep-sea relatives of these cave species (Macpherson and Segonzac 2005; Parapar et al. 2011; Pettibone 1989). Alternatively, the crevicular system of Lanzarote might extend deep along the island building and provide physical connectivity between the island and the surrounding deep-sea environments (Iliffe 1990). In this scenario, cave colonization might have been facilitated by the ecological similarities between cave and deep-sea environments, both characterized by total darkness, constant temperature, and low oxygen (Danielopol et al. 1996).

5 Conservation Challenges and Sustainable Uses of the Anchialine Environments

Anchialine habitats, like many other natural splendors, are highly susceptible to negative anthropogenic impacts. In Lanzarote, the main impact derives from recreational uses of the anchialine environments, but other potentially harmful activities are unregulated animal collections for scientific or expositive purposes, as well as the uncontrolled use of the land especially in the areas nearby the lava field of La Corona.

Recreational uses. Anchialine ecosystems in Lanzarote are threaten by unappropriated recreational uses both by locals and tourists. Cueva de Los Lagos is often visited without authorization by small groups of people with an inherent risk both for the environment and the visitors, who often lack the appropriated equipment and training. Vandalism acts and garbage dumped in the passageways, as well as sunscreen and other cosmetic products polluting the anchialine lakes are the undesirable consequences of most of these visits (Martínez et al. 2016). Local authorities have installed different types gates during the years to protect the entrance, but all have been forced open and illegal visits continue (Núñez and Brito 2008a, b).

The touristic center of Los Jameos del Agua has been one the major touristic attractions of Lanzarote since the 1970s and receives thousands of visitors every month (Centro de Datos de Lanzarote 2017). The touristic center protects the anchialine lake from uncontrolled visitation, dumping of trash, and acts of vandalism, but as a counterpart exposes it to other types of anthropogenic threats. These threats mostly revolve around the intentional tossing of coins into the lake by visitors who regard this water body as a natural ‘wishing well’, despite the displayed signs forbidding such activities (Brito et al. 2009). The occasional dropping of random objects, evening musical events, and periodical festivals may also potentially have detrimental effects on these fragile ecosystems. While to date the populations of the endemic species in the lake show no signs of stress, preliminary research has detected very high concentration of heavy metals in the sediments that might eventually carry deadly effects on the fauna (Núñez and Brito 2008a). Additionally, the presence of heavy metals might facilitate the co-selection of antibiotic resistance genes in bacterial communities of the lake, as it has been showed elsewhere (Di Cesare et al. 2016). Scientist are working along with the local authorities and the administration of the touristic center to understand the cumulative effects of all these disturbances and minimizing possible long-lasting effects.

Collection of cave animals. Collections of cave animals with scientific or exposition purposes might have harmful effects on certain the stygobitic population (Núñez and Brito 2008a, b). *Munidopsis polymorpha* and *Morlockia ondinae* are considered endangered and can only be collected after permission granted by the local governments. The collection of other cave species remains unregulated. However, lack of information on biology and life cycles of most of these species complicates the establishment of efficient regulations, which minimize the negative impact over their fragile populations.

Use of surrounding terrains. Any anthropogenic access to terrains surrounding anchialine ecosystems, either for commercialization, construction, agriculture, mineral exploitation, or water resources via bore holes or wells has the potential to introduce contamination, ultimately impacting the underlying anchialine system (Iliffe et al. 1984a). Likewise, due to the interconnectivity between Lanzarote’s anchialine system and the ocean, even activities several kilometers away from the island may have detrimental effects, especially with regards to those contaminants capable of entering the system by tidal pumping. Given that the majority of species living within these habitats have limited distributions and highly specific habitat requirements, any of these activities is likely to have conservation implications.

Many anchialine systems occur in tropical and subtropical areas, such as México, Bahamas, and Bermuda, where the push for development of tourism increased risks derived from land use. Fortunately, Lanzarote has adopted a sustainable touristic development since the 1970s partly due to work of the artist César Manrique, who promoted an integrative touristic model that minimizes the negative impact on the landscape and nature (Pezzi 2013). Furthermore, in the 1990s several areas of Lanzarote, including La Corona lava field and Los Jameos del Agua, were integrated and protected within the Red Canaria de Espacios Protegidos, which regulates human activities and prohibits major alterations in these areas. The efforts for conservation reached a milestone in 1993, when Lanzarote was declared an UNESCO Biosphere Reserve, and in 2015 when it was integrated within the UNESCO Global Geopark of Lanzarote and the Chinijo Islands. Today, these institutions and the local government work along with scientists performing state-of-art biological and geological research that allows the implementation of evidence-based policies, which, amongst many other benefits, will ensure a better understanding of the anchialine ecosystems that ensure its preservation through time.

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