Daniel F.R. Cleary, Yusheng M. Huang, Nicole, J. de Voogd. A marine karst ecosystem in need of some love. *Journal of Cave and Karst Studies*, v. 87, no. 3, p. 95-104. DOI:10.4311/2023EX0120

A MARINE KARST ECOSYSTEM IN NEED OF SOME LOVE

Daniel F.R. Cleary[1C], Yusheng M. Huang[2], Nicole, J. de Voogd[3,4C]

ABSTRACT: Here we describe a shallow-water karst ecosystem observed along the coast of Taiwan's Orchid Island, consisting of extensive networks of caves, canyons, and pools. Measurements at various locations in two pools revealed marked gradients in nutrients, temperature, and salinity, indicative of submarine, relatively nutrient-rich, and terrestrially-derived groundwater discharge into the coastal marine environment. Within these pools, dead coral formations dominated at land-adjacent locations, whereas mid- and sea-adjacent locations housed assemblages of corals, algae, and sponges. Several caves were found to house a rich variety of sponges, including 17 species that are potentially new to science. The sponge fauna included sclerosponges, which are hard, coral-like, atypical sponges that combine calcareous and siliceous skeletal parts. Other notable species included the recently described *Vetulina incrustans* and potentially new species belonging to the lithistid family, Theonellidae. Additionally, the caves housed red macroalgae and ahermatypic corals. The singular ecosystem currently receives no formal protection, and parts of it are adjacent to a nuclear storage waste facility. Overall, our study revealed that the cave and pool system houses a complex and diverse marine community of uncommon organisms, including a large number of potentially new species, highlighting its ecological significance.

INTRODUCTION

There is a Dutch expression, "*onbekend maakt onbemind*," which translates to "unknown makes unloved." The unknown is unloved, ignored. This sentiment is particularly pertinent to nature conservation. With the loss of habitats or ecosystems, many smaller, obscure species may be lost forever without us ever having known that they existed (Boehm and Cronk, 2021). In some instances, whole habitats or ecosystems may be unknown, ignored, and placed at risk. In the present study, we discuss one such ecosystem: a shallow-water marine karst ecosystem located along the coast of Orchid Island, Taiwan. Although there have been several studies of the coral reefs surrounding Orchid Island (Chao, 2002; Chao and Lee, 2002; Chen et al., 2002; Kao et al., 2007; Lee, 1980; Lee and Lee, 1981; Reigle, 1963; Yu, 1985), the pool and cave systems have, thus far, been largely ignored, at least from a scientific perspective.

Marine karst areas, which consist of pools, crevices, and caves, are unique habitats that are both fascinating and scientifically important. They are known for their diverse communities of organisms, including algae, sponges, other invertebrates, and vertebrates, as well as for their stunning geological features, which often include intricate rock formations. The areas are also popular destinations for diving and ecotourism and have been the focus of scientific studies (Sket, 1996; Harmelin, 1997). Located along rocky, karst coastlines, shallow water caves are exposed during low tide and covered by seawater during high tide. They support distinct and diverse communities of organisms adapted to survive in environments subject to marked fluctuations in temperature, light levels, and salinity (Sket, 1996; Meroz-Fine et al., 2005). One of the most interesting aspects of these systems is the way in which different species have adapted to the challenges posed by such environments. For example, certain species inhabiting caves may have evolved to survive in complete darkness, while others developed the ability to photosynthesize at very low light levels (Bibiloni et al., 1989; Radolović et al., 2015; Mayer et al., 2016; Tzabari et al., 2018). Species of invertebrates inhabiting these ecosystems often have to adapt to rapid changes in temperature and salinity, as well as the limited resources available in cave environments. Caves can also contain taxa otherwise restricted to deep-sea environments, as exemplified by the discoveries of carnivorous and glass sponges in several Mediterranean caves (Bakran Petricioli et al., 2007; Vacelet, 1996; Vacelet et al., 1994). Another reason why marine karst ecosystems are of such interest is the potential they have for discovering rare and previously undescribed species, including large numbers of endemics (Manconi and Serusi, 2008; Iliffe and Kornicker, 2009; Gerovasileiou et al., 2015).

Sponges are among the most abundant and diverse organisms that inhabit marine karst ecosystems. They are crucial components of these ecosystems, providing habitat and food for other cave-dwelling species (Gerovasileiou et al., 2016; Pisera and Gerovasileiou, 2021). Gerovasileiou and Voultsiadou (2012) conducted an exhaustive literature review of 133 publications and 185 caves, spanning more than 60 years of research. They recorded 311 sponge

[1]Department of Biology and CESAM, University of Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal; Orcid DFR Cleary: 0000-0002-6143-3390
[2]Department of Marine Recreation, National Penghu University of Science and Technology, Penghu, Taiwan
[3]Naturalis Biodiversity Center, Leiden, The Netherlands; Orcid NJ de Voogd: 0000-0002-7985-5604
[4]Institute of Biology (IBL), Leiden University, the Netherlands
[C]Corresponding authors; address correspondence to cleary@ua.pt or n.j.de.voogd@biology.leidenuniv.nl

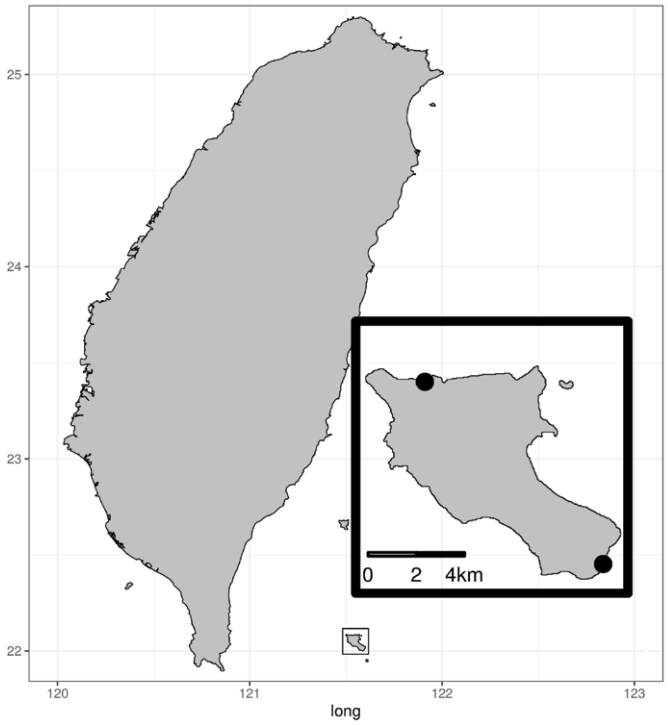

Fig. 1. Map of research area showing location of Orchid Island with respect to Taiwan and sites where environmental variables were measured in pools (inset).

species, representing almost half of the total sponge species across the Mediterranean, which is considered a biodiversity hotspot. Additionally, sponges are known to play important roles in the cycling of nutrients and energy in these environments (Slattery et al., 2013; Maldonado, 2016). Beyond the previously mentioned Mediterranean studies, recent research has identified new species of sponges from karst systems in Japan and Polynesia (Schuster et al., 2021; Ise et al., 2023).

In this study, we describe a shallow-water, marine karst pool and cave system located on Orchid Island, Taiwan. We describe the environmental conditions in two pools and provide a preliminary list of sponge species sampled from several locations along the coast (Table 1), which included 17 potentially novel species. In a companion study, we described the prokaryotic communities associated with sponges from cave, pool, and proximate coral reef habitats (Cleary et al. 2024). This is the first study to describe the environmental conditions of the system.

METHODS

Orchid Island (also known as Lanyu Island; Fig. 1) is located 98 km off the Southeast coast of Taiwan at the edge of the Asian and Philippine Sea tectonic plates. In contrast to the island of Taiwan itself, Orchid Island lies on the Philippine Sea plate (Inoue et al., 2011). A karst ecosystem comprising an intricate network of pools, caves, and canyons surrounds parts of the island. It is partially separated from the mainland by a drab gray concrete wall (Fig. 2a). The caves are subject to daily ebb and flow in addition to periodic severe storm events, including frequent typhoons, with considerable wave energy (pers. obs. Daniel Cleary). The karst ecosystem differed from previous karst systems we had visited (Becking et al., 2013; Cleary and Polónia, 2018, 2020; Cleary and Gomes, 2019; Cleary et al., 2016, 2020; Ferreira et al., 2020) and typical karst coasts as described in Paskoff (2005) and van Hengstum et al. (2019). The shallow caves we observed presented a unique opportunity to easily study cave flora and fauna in a highly dynamic marine environment. The caves and pools were studied using snorkeling and SCUBA diving. Organisms were sampled from pools and caves, and the samples were preserved in 96 % ethanol, with a focus on sponges, and subsequently sent to the Naturalis Biodiversity Center in the Netherlands. The sponges were identified by Nicole de Voogd using classical morphological characters and DNA barcodes. Voucher specimens have been deposited in the sponge collection of Naturalis Biodiversity Center (as RMNH POR#).

In addition to sampling the flora and fauna, environmental variables were measured. Concentrations of ammonia, nitrite, nitrate, phosphate, and salinity were measured at three locations within the Yayo tidal pool: land-adjacent, mid-pool, and open sea-adjacent (the portion of the pool closest to the sea), as well as at a nearby open-sea coral reef ecosystem. The distance between the land-adjacent and open sea-adjacent locations in the Yayo pool was approximately 54 m. The pool itself was separated from the open sea by a shallow water, cave system that consisted of an intricate network of smaller and larger caves with differing degrees of illumination in addition to extensive canyon-like structures (Fig. 2a). Three replicate water samples were collected from each location in the pool and the coral reef using Niskin bottles on October 10, 2018. For each sample, 50 ml of water was filtered using a sterile 0.20 µm PES filter. The filters were stored in sterile 10 mL Falcon tubes and frozen at –20 °C. Using these samples, dissolved inorganic nitrogen ($[NH_4]^+$, NO^-, and DIN), $[PO_4]^{3-}$, and salinity were measured at the Royal Netherlands Institute for Sea Research (NIOZ), the Netherlands, using an AxFlow Bran+Luebbe Traacs800 auto-analyzer. Time series of temperature, pH, and oxidation reduction potential (ORP with units mV) were measured in two pools (Yayo tidal pool and Secret of Iraralay pool) at land-adjacent and sea-adjacent locations within each pool. The measurements were taken using a T7-1 reef datalogger (DASCOR, Inc., Oceanside, CA, USA) from July 28 to August 11, 2019 at the Yayo (Latitude:22.0076179, Longitude:121.5946121) and the Secret of Iraralay (22.0813281, 121.5225911) pools. In addition to these two sites, sponges were also sampled from Lady's Rock cave (22.0835444, 121.5258043), Longman Harbour (22.0043515, 121.5799323), Yayo pool 2 (22.0080886, 121.5946905), Shells and pool (22.0750278, 121.5680538), Jikarahem pool (22.0817145, 121.5113184), and Jitalan Talan (22.0800747, 121.5595633). A playlist of drone videos of Orchid Island

Table 1. List of sponge species sampled from cave and pool habitats of Orchid Island.

Class	Subclass	Order	Family	Genus	Species	Source
Calcarea	Calcaronea	Leucosolenida	Amphoriscidae	Paraleucilla	sp.	
Calcarea	Calcaronea	Leucosolenida	Grantiidae	Grantia	sp.	
Calcarea	Calcaronea	Leucosolenida	Grantiidae	Leucandra	sp.	
Calcarea	Calcaronea	Leucosolenida	Granttidae	Ute	sp.	
Calcarea	Calcinea	Clathrinida	Clathrinidae	Borojevia	sp.	
Calcarea	Calcinea	Clathrinida	Clathrinidae	Janusya	sp.	
Calcarea	Calcinea	Clathrinida	Dendyidae	Ascandra	sp.	
Calcarea	Calcinea	Clathrinida	Leucettidae	Leucetta	chagosensis	Dendy, 1913
Demospongiae	Heteroscleromorpha	Agelasida	Agelasidae	Acanthostylotella	cornuta	(Topsent, 1897)
Demospongiae	Heteroscleromorpha	Agelasida	Agelasidae	Agelas	sp.nov.	
Demospongiae	Heteroscleromorpha	Agelasida	Astroscleridae	Astrosclera	willeyana	Lister, 1900
Demospongiae	Heteroscleromorpha	Axinellida	Axinellidae	Phycopsis	sp.	
Demospongiae	Heteroscleromorpha	Axinellida	Heteroxyidae	Myrmekioderma	sp.	
Demospongiae	Heteroscleromorpha	Axinellida	Raspailiidae	Didiscus	sp.	
Demospongiae	Heteroscleromorpha	Biemnida	Biemnidae	Biemna	sp.	
Demospongiae	Heteroscleromorpha	Clionaida	Placospongiidae	Placospongia	carinata	(Bowerbank, 1858)
Demospongiae	Heteroscleromorpha	Clionaida	Placospongiidae	Placospongia	mixta	Thiele, 1900
Demospongiae	Heteroscleromorpha	Clionaida	Spirastrellidae	Spirastrella	sp.	
Demospongiae	Heteroscleromorpha	Clionaida	Acanthochaetetidae	Acanthochaetetes	wellsi	Hartman & Goreau, 1975
Demospongiae	Heteroscleromorpha	Haplosclerida	Chalinidae	Haliclona	sp.	
Demospongiae	Heteroscleromorpha	Haplosclerida	Petrosiidae	Neopetrosia	sp.	
Demospongiae	Heteroscleromorpha	Haplosclerida	Petrosiidae	Petrosia	alfiani	de Voogd & van Soest, 2002
Demospongiae	Heteroscleromorpha	Haplosclerida	Petrosiidae	Petrosia	corticata	(Wilson, 1925)
Demospongiae	Heteroscleromorpha	Haplosclerida	Petrosiidae	Petrosia	microxea	(Vacelet, Vasseur & Lévi, 1976)
Demospongiae	Heteroscleromorpha	Haplosclerida	Petrosiidae	Petrosia	sp.	
Demospongiae	Heteroscleromorpha	Haplosclerida	Petrosiidae	Xestospongia	sp.nov.	
Demospongiae	Heteroscleromorpha	Poecilosclerida	Mycalidae	Mycale	sp.	
Demospongiae	Heteroscleromorpha	Poelicosclerida	Coelocarteriidae	Coelocarteria	agglomerans	Azzini, Calcinai & Pansini, 2007
Demospongiae	Heteroscleromorpha	Polymastiida	Polymastiidae	Polymastia	sp.	
Demospongiae	Heteroscleromorpha	Polymastiida	Polymastiidae	Pseudotrachya	sp.nov.	
Demospongiae	Heteroscleromorpha	Scopalinida	Scopalinidae	Svenzea	sp.nov.	
Demospongiae	Heteroscleromorpha	Sphaerocladina	Vetulinidae	Vetulina	incrustans	Schuster, Pisera & Kelly, 2018
Demospongiae	Heteroscleromorpha	Suberitida	Halichondriidae	Axinyssa	sp.	
Demospongiae	Heteroscleromorpha	Suberitida	Halichondriidae	Hymeniacidon	sp.	
Demospongiae	Heteroscleromorpha	Suberitida	Suberitidae	Aaptos	sp.nov.	

Table 1. List of sponge species sampled from cave and pool habitats of Orchid Island.

Class	Subclass	Order	Family	Genus	Species	Source
Demospongiae	Heteroscleromorpha	Suberitida	Suberitidae	Terpios	hoshinota	Rützler & Muzik, 1993
Demospongiae	Heteroscleromorpha	Tethyida	Tethyidae	Tethytimea	sp.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Ancorinidae	Asteropus	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Ancorinidae	Dercitus (Stoeba)	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Ancorinidae	Rhabdastrella	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Corallistidae	Neophrissospongia	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Geodiidae	Erylus	sp.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Geodiidae	Penares	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Neopeltidae	Sollasipelta	ornata	(Sollas, 1888)
Demospongiae	Heteroscleromorpha	Tetractinellida	Scleritodermidae	Aciculites	ciliata	Wilson, 1925
Demospongiae	Heteroscleromorpha	Tetractinellida	Scleritodermidae	Microscleroderma	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Scleritodermidae	Scleritoderma	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Siphonidiidae	Gastrophanella	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Tetillidae	Acanthotetilla	sp.nov.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Tetillidae	Cinachyra	sp.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Tetillidae	Cinachyrella	sp.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Tetillidae	Craniella	sp.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Tetillidae	Paratetilla	sp.	
Demospongiae	Heteroscleromorpha	Tetractinellida	Theonellidae	Manihinea	sp.nov.	
Demospongiae	Heteroscleromorpha	Theonellidae	Theonellidae	Theonella	mirabilis	(de Laubenfels, 1954)
Demospongiae	Heteroscleromorpha	Theonellidae	Theonellidae	Theonella	sp.nov.	
Demospongiae	Homoscleromorpha	Homosclerophorida	Plakinidae	Plakina	sp.nov.	
Demospongiae	Homoscleromorpha	Homosclerophorida	Plakinidae	Plakinasterella	sp.	
Demospongiae	Homoscleromorpha	Homosclerophorida	Plakinidae	Plakortis	sp.	
Demospongiae	Keratosa	Dictyoceratida	Dysideida	Dysidea	sp.	
Demospongiae	Keratosa	Dictyoceratida	Dysideida	Lamellodysidea	herbacea	(Keller, 1889)
Demospongiae	Keratosa	Dictyoceratida	Thorectidae	Cacospongia	mycofijiensis	(Kakou, Crews & Bakus, 1987)
Demospongiae	Keratosa	Verongiida	Aplysinellidae	Suberea	sp.	
Demospongiae	Verongimorpha	Chondrillida	Chondrillidae	Chondrilla	grandistellata	Thiele, 1900
Demospongiae	Verongimorpha	Chondrillida	Chondrillidae	Chondrosia	sp.	

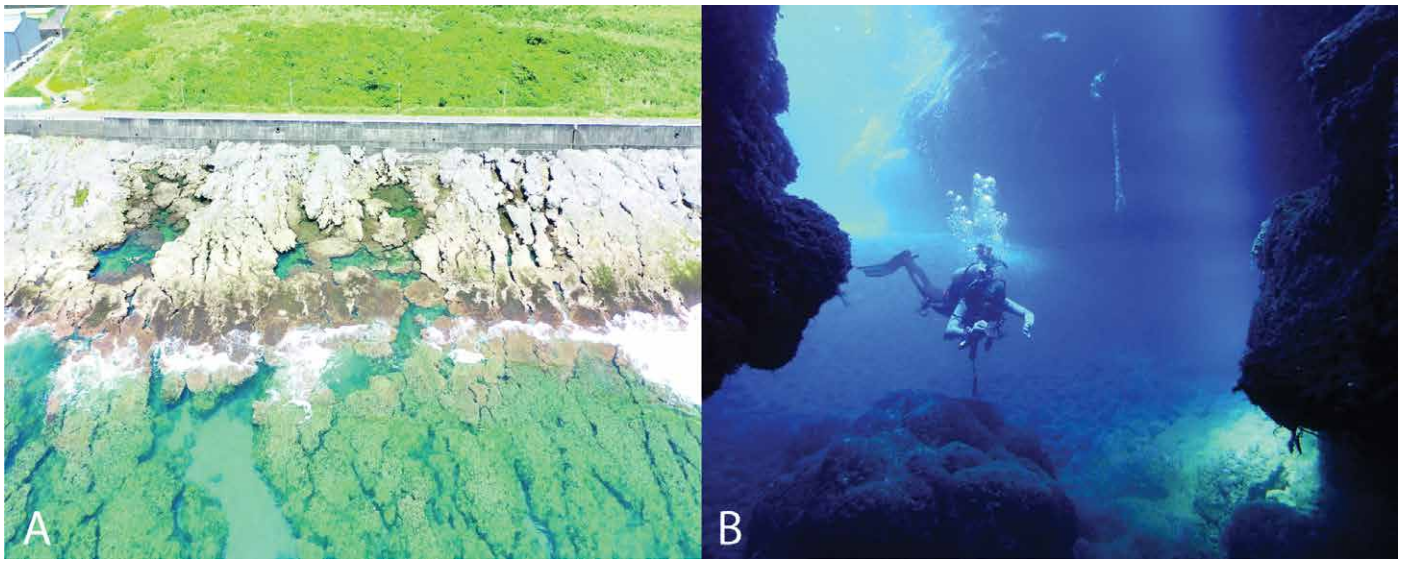

Fig. 2. Bird's-eye view image made by a drone of the karst ecosystem and the Yayo tidal pools. The photograph was taken by JKZ Cleary on July 31, 2019, next to the Orchid Island nuclear waste station. b. Photograph taken at the cave entrance of a large karst pool (Yayo tidal pool). The photograph was taken by NJ de Voogd on July 29, 2019.

and underwater videos of caves is available at: https://tinyurl.com/5jmnrzca (accessed April 18, 2024).

RESULTS

There were pronounced gradients in several environmental parameters within the pools (Figs. 3 and 4). Concentrations of nitrate and phosphate declined precipitously from the land-adjacent location of Yayo tidal pool to the mid-pool and open sea-adjacent locations and reached lowest levels in the open sea, coral reef location (Fig. 3). Concentrations of ammonia and nitrite initially increased from the land-adjacent to the mid- and sea-adjacent locations in the pools. However, they were lowest at the coral reef location. Salinity increased from the land-adjacent location to the mid-pool and open sea-adjacent locations, and was highest in the open sea and coral reef locations. The land-adjacent locations of both the Yayo and Secret of Iraralay pools were characterized by lower temperatures and pH values and markedly higher fluctuations in both parameters than the open sea-adjacent locations (Fig. 4). The oxidation-reduction potentials were consistently higher (less negative) at the open sea-adjacent sites of both pools. Our results suggest

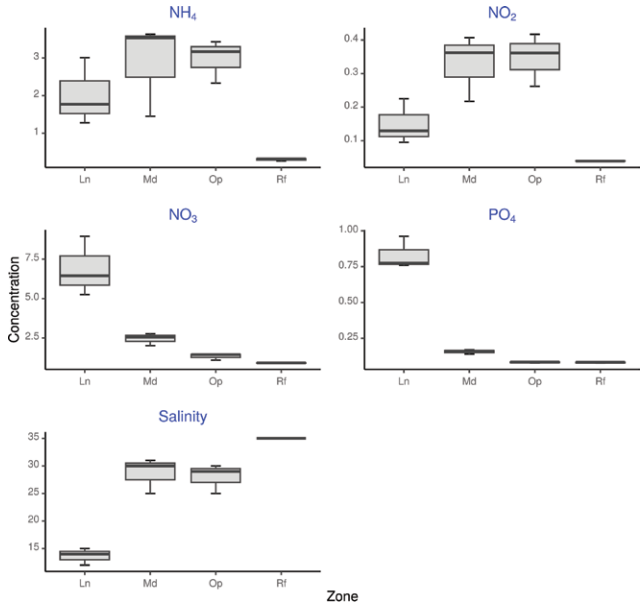

Fig. 3. Concentrations of ammonium, nitrite, nitrate, phosphate, and salinity sampled at land-adjacent (Ln), mid-pool (Md), and open sea-adjacent (Op) sites in the large Yayo pool and a proximate coral reef (Rf) site.

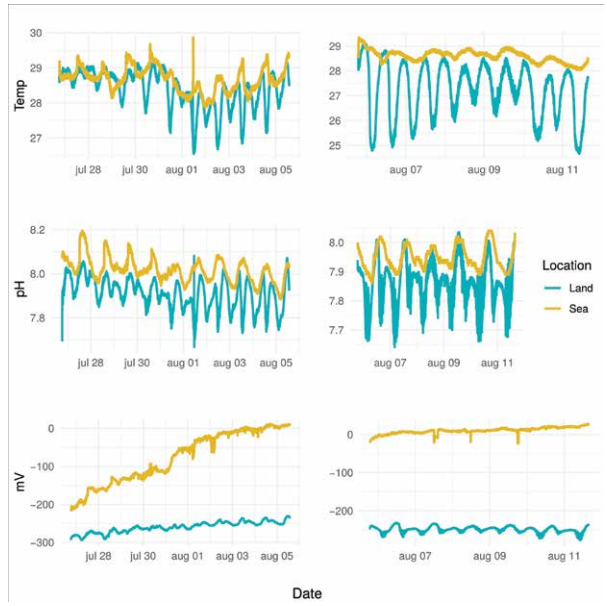

Fig. 4. Temperature, pH, and oxidation reduction potential (measured in mV) sampled in the Yayo and Secret of Iraralay pools at land-adjacent and open sea-adjacent sites during July and August, 2019.

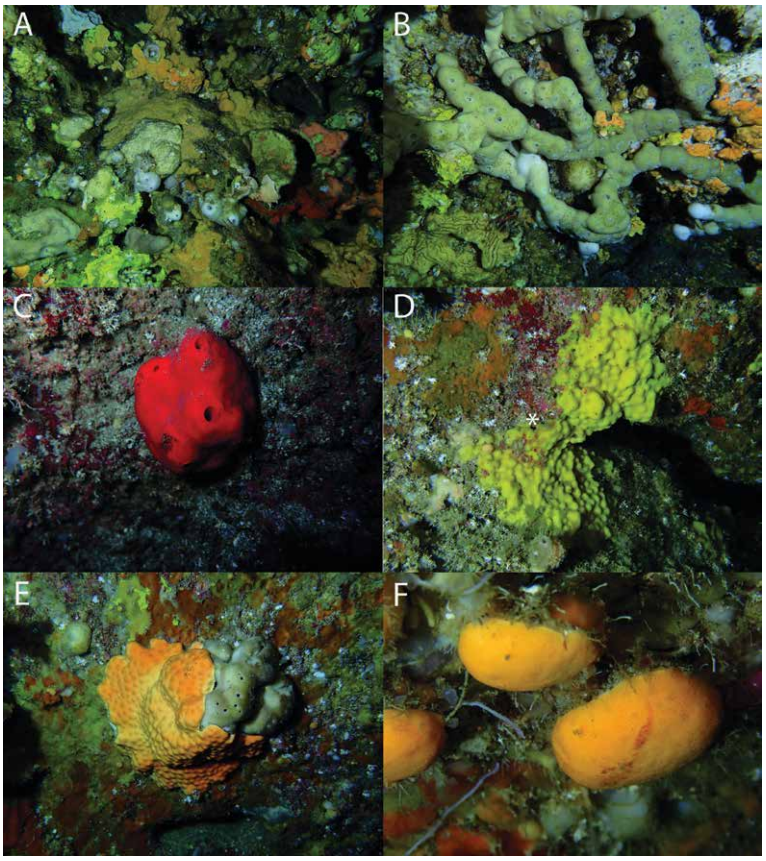

Fig. 5. A. Dense aggregations of potentially new sponge species and sclerosponges. Photograph taken by NJ de Voogd at Longman Harbour, Orchid Island, Taiwan, on July 30, 2019. B. Several sponge species growing on a cave wall. Photograph taken by NJ de Voogd at Lady's Rock cave, Orchid Island, Taiwan, on July 27, 2019. C. Potentially new species of Manihinea. Photograph taken by NJ de Voogd in a cavern close to the Orchid Island nuclear waste facility, Taiwan, on August 13, 2018. D. Image showing a specimen of the sponge species *Vetulina incrustan*s. Photograph taken by NJ de Voogd at the Orchid Island Shell and Pool, Taiwan, on August 1, 2019. E. Image of *Acanthochaetetes wellsi* overgrowing a potentially new species of *Neophrissospongia*. Photograph taken by NJ de Voogd at the Orchid Island Shell and Pool, Taiwan, on the 1st of August 2019. Image of *Astrosclera willeyana* taken by NJ de Voogd at Lady's Rock cave, Orchid Island, Taiwan, on July 27, 2019.

that the groundwater discharge entering the marine environment is relatively nutrient-rich and characterized by lower temperatures and pH values.

The change in environmental parameters along the land-to-sea gradient was also visually evident within the pools, with dead coral formations dominating near the land, including small caves and crevices with sparse algal and invertebrate encrustations. These were somewhat abruptly replaced by diverse assemblages of hard and soft corals, algae, and sponges in the mid-pool and sea-adjacent locations. These, in turn, were replaced by dense incrustations of sponges and other organisms as light levels declined upon entering the caves, which separated the pools from the open sea.

Initial investigations of the caves (Fig. 2b) revealed an exceptionally rich flora and fauna, characterized by dense and diverse assemblages of sponges covering parts of the cave walls (Fig. 5). Videos of the cave fauna are available as a playlist: https://tinyurl.com/5jmnrzca (accessed April 18, 2024). Subsequent taxonomic analysis revealed that many of these sponges are potentially new to science. Thus far, a total of 17 potentially novel species have been identified, including species in the lithistid sponge genera *Scleritoderma* and *Neophrissospongia*, as well as demosponges in the genera *Svenzea* and *Acanthotetilla*, and several calcareous sponges. Important structural components of the sponge fauna were two species of sclerosponges (*Astrosclera willeyana* and *Acanthochaetetes wellsi*). Unlike most sponges, sclerosponges (Fig. 6) are hard, coral-like, and consist of a thin layer of living tissue surrounding an aragonite or calcite mass that encloses small siliceous spicules (Hartman, 1983; Willenz and Hartman, 1989; Asami et al., 2020; Grottoli et al., 2020). Sclerosponges are primarily restricted to deep-water habitats, although they have been found in shallower waters in several locations worldwide (Karlińska-Batres and Wörheide, 2015). Sclerosponges were common reef-building organisms during the late Palaeozoic and Mesozoic eras. Certain modern sclerosponges are morphologically similar to these now-extinct species; thus, they are often considered living fossils (Basile et al., 1984; Vacelet, 1985; Asami et al., 2021). Modern sclerosponges are both slow-growing and long-lived (up to a thousand years) and can contribute to reef-building; they are also used as proxies for paleoceanographic reconstruction (Lang et al., 1975; Asami et al., 2020; Macartney et al., 2020). The morphology of *A. wellsi* in the caves of Orchid Island differed substantially from that observed from Saipan, Palau, and the Marshall Islands (Hartman and Goreau, 1975; Ogawa et al., 1993; Quinn and Kojis, 1999; Grottoli et al., 2006). Instead of the typical, half-spherical growth form, the specimens in the Orchid Island caves often formed large spikes (Fig. 6).

In our study area, sclerosponge formations extended from semi-dark cave habitats to canyon-like structures, encompassing a diverse array of sponge species. Sclerosponges have also been observed at Kume Island and the Ryukyu Islands (Japan), and we suspect that similar cave systems exist in nearby cave systems in Japan and the Philippines. In addition to sclerosponges, the caves housed several species of lithistids, an ancient group of sponges that have been the subject of chemical investigation for their pharmaceutical properties (Bewley and Faulkner, 1998; Kogawa et al., 2022; Holland et al., 2023). The lithistid species included several potentially new species belonging to the lithistid family Theonellidae, including potentially novel *Theonella* species and a *Manihinea* species. The potentially novel *Manihinea* species is particularly conspicuous, with a bright red color. Only two *Manihinea* species have been described thus

Fig. 6. Photograph of a sclerosponge *(Acanthochaetetes wellsi)* taken in a cavern close to the Orchid Island nuclear waste facility by DFR Cleary on October 10, 2018.

Fig. 7. Photograph showing the Yayo tidal pool in the vicinity of the nuclear dump site, taken by DFR Cleary on October 9, 2018.

Fig. 8. Photograph showing the karst ecosystem bordering the nuclear dump site at the southern tip of Orchid Island, taken by JKZ Cleary on July 31, 2019. The island of Hsiao Lanyu can be seen in the distance.

far, and both were collected from mesophotic depths. *Manihinea lynbeazleyae* Fromont and Pisera, 2011, was collected in Western Australia at a depth of 194–203 m, and *Manihinea conferta* Pulitzer-Finali, 1993, was collected in Kenya at a depth of 90–100 m. Although the colour of *M. conferta* is not given, *M. lynbeazleyae* has a similar color, namely bright orange-red. Other interesting species included *Vetulina incrustans,* recently described from specimens collected deep inside crevices at a depth of 7–12 m in the Philippines (Schuster et al., 2018). The genus *Vetulina* is the sole living representative of a once-diverse Mesozoic sponge group, representing a relict species that originated from the Tethys Sea (Schuster et al., 2018).

The cave systems represent a unique and potentially valuable habitat. Thus far, we have identified six pools with adjacent cave and canyon systems, as well as a cave located in slightly deeper water further from the coast. In addition to sponges, algae and ahermatypic corals were also observed inside the caves. Coral reefs, interspersed with sand flats, were observed in relative proximity to the caves. The coral reefs consisted of typical scleractinian and sponge species among the other normal denizens of coral reefs. The shallow-water caves and pools observed in their present form are part of a large network of rock formations that exist at the land-sea interface.

DISCUSSION

Much of the shallow water karst ecosystem of Orchid Island remains to be fully explored, and the darker recesses may, in their own right, represent a unique and hitherto unexplored cave system along a freshwater-to-saline gradient. At present, it is important to categorize and identify the extent of the entire system further, in addition to collecting and identifying potentially novel species. Given the unique nature of this ecosystem, ensuring its future protection is crucial. Intertidal cave systems face numerous threats due to their location along coastlines (Nepote et al., 2017; Montefalcone et al., 2018). Disturbances affecting coastal habitats, in general, also pose a threat to intertidal cave systems. These include chemical pollutants such as pesticides and heavy metals, as well as plastic waste and sewage. Similar marine

cave habitats in the Mediterranean are considered endangered and are protected by the European and Mediterranean legislative framework due to their unique biological wealth (Giakoumi et al., 2013).

Habitat destruction (e.g., loss of adjacent coral reefs, seagrass fields, mangrove or coastal forests) can indirectly or directly affect cave systems. Tourism, in turn, may pose a direct threat when unwary tourists inadvertently destroy slow-growing cave species. The pool and cave systems of Orchid Island currently receive no formal protection, while the pools are frequented by large groups of tourists. Furthermore, the two most prominent pools (Fig. 7) and their adjacent cave systems lie directly adjacent to a nuclear storage facility (Fig. 8). Nuclear waste was brought to Orchid Island from 1982 to 1996 and currently amounts to 97,671 barrels. The indigenous inhabitants of Orchid Island were also initially unaware of the storage facility (Huang et al., 2013). An important component of protecting the karst ecosystem will be to ensure it is shielded from nuclear leakage and other potentially harmful effluents emanating from the island. Perhaps if the unique nature and beauty of Orchid Island's karst ecosystem had been known at the time, this would have dissuaded the Taiwanese authorities from storing almost 100,000 barrels of nuclear waste at its edge.

ACKNOWLEDGEMENTS

Katherine Liao, Yi-Chin Wu, Martin van der Plas, Astrid Verkerk, Floris, and Julian Cleary are thanked for their help in the field. We would also like to thank Tung Lung Diving for their help and support. Julian Cleary is thanked for making bird's-eye view images using the Mavic 2-Pro. We thank Jan van Ojijen (NIOZ) for his assistance with the water sample analyses. This research was facilitated by generous support from the National Science and Technology Council to Yusheng Huang (110-2621-B-346-001) and from the research program NWO-VIDI with project number 16.161.301 to Nicole de Voogd, which is financed by the Netherlands Organization for Scientific Research (NWO). This work was supported by European Funds through COMPETE [FCOMP-01-0124-FEDER-008657] and by National Funds through the Portuguese Foundation for Science and Technology (FCT) within the LESS CORAL [PTDC/AAC-AMB/115304/2009] project. We acknowledge financial support to CESAM from FCT/MCTES (UIDP/50017/2020+ UIDB/50017/2020 + LA/P/0094/2020) through national funds.

Authorship statement: DFR Cleary and NJ de Voogd wrote the initial document. YM Huang provided comments on the document. DFR Cleary, NJ de Voogd, and YM Huang performed the fieldwork.

REFERENCES

Asami, R., Kinjo, A., Ohshiro, D., Naruse, T., Mizuyama, M., Uemura, R., Shinjo, R., Ise, Y., Fujita, Y., and Sakamaki, T., 2020, Evaluation of geochemical records as a paleoenvironmental proxy in the hypercalcified demosponge *Astrosclera willeyana*: Progress in Earth and Planetary Science, v. 7, no. 1, p. 1–18. https://doi.org/10.1186/s40645-020-00329-z

Asami, R., T. Matsumori, R. Shinjo, R. Uemura, Y. Miyaoka, M. Mizuyama, Y. Ise, and T. Sakamaki, 2021, Reconstruction of ocean environment time series since the late nineteenth century using sclerosponge geochemistry in the northwestern subtropical Pacific: Progress in Earth and Planetary Science, v. 8, no. 1, p. 1–16. https://doi.org/10.1186/s40645-021-00434-7

Bakran Petricioli, T., J. Vacelet, H. Zibrowius, D. Petricioli, P. Chevaldonné, and T. Rada, 2007, New data on the distribution of the 'deep sea' sponges *Asbestopluma hypogea* and *Oopsacas minuta* in the Mediterranean Sea: Marine Ecology, v. 28, no. s1, p. 10–23. https://doi.org/10.1111/j.1439-0485.2007.00179.x

Basile, L. L., R. J. Cuffey, and D. F. Kosich. 1984. Sclerosponges, pharetronids, and sphinctozoans (relict cryptic hard-bodied Porifera) in the modern reefs of Enewetak Atoll: Journal of Paleontology, v. 58 no. 3, 636–650.

Becking, L. E., D. F. R. Cleary, and N. J. de Voogd, 2013, Sponge species composition and abundance in the mangroves and marine lakes of Berau, Indonesia: Marine Ecology Progress Series, v. 481, p. 105–120. https://doi.org/10.3354/meps10155

Bewley, C. A., and D. J. Faulkner, 1998, Lithistid sponges: star performers or hosts to the stars: Angewandte Chemie International Edition, v. 37, no. 16, p. 2162–2178. https://doi.org/10.1002/(SICI)1521-3773(19980904)37:16<2162::AID-ANIE2162>3.0.CO;2-2

Bibiloni, M. A., M. J. Uriz, and J. M. Gili, 1989, Sponge communities in three submarine caves of the Balearic Islands (Western Mediterranean): adaptations and faunistic composition: Marine Ecology, v. 10, no. 4, p. 317–334. https://doi.org/10.1111/j.1439-0485.1989.tb00076.x

Boehm, M. M. A., and Q. C. B. Cronk, 2021, Dark extinction: the problem of unknown historical extinctions: Biology Letters, v. 17, no. 3, p. 20210007. https://doi.org/10.1098/rsbl.2021.0007

Chao, S.-M., 2002, The shallow-water echinoderms from Lanyu, Taiwan: Collection and Research, v. 15, p. 1–7.

Chao, S.-M., and S.-C. Lee, 2002, Marine shells from Lanyu, Taiwan: Collection and Research, v. 15, p. 9–33.

Chen, C. A., N. V. Wei, and C. F. Dai, 2002, Genotyping the clonal population structure of a gorgonian coral, *Junceella fragilis* (Anthozoa: Octocorallia: Ellisellidae) from Lanyu, Taiwan, using simple sequence repeats in ribosomal intergenic spacer: Zoological Studies, v. 41, no. 3, p. 295–302.

Cleary, D. F. R., and N. C. M. Gomes, 2019, Bacterial, archaeal and microeukaryote plankton communities inside and outside of Indonesian marine lakes: Journal of Sea Research, v. 148–149, p. 23–32. https://doi.org/10.1016/j.seares.2019.04.001

Cleary, D. F. R., and A. R. M. Polónia, 2018, Bacterial and archaeal communities inhabiting mussels, sediment and water in Indonesian anchialine lakes: Antonie van Leeuwenhoek Journal of Microbiology, v. 111, p. 237–257. https://doi.org/10.1007/s10482-017-0944-1

Cleary, D. F. R., and A. R. M. Polónia, 2020, Marine lake populations of jellyfish, mussels and sponges host compositionally distinct prokaryotic communities: Hydrobiologia, v. 847, p. 3409–3425. https://doi.org/10.1007/s10750-020-04346-3

Cleary, D. F. R., L. E. Becking, A. R. M. Polónia, R. Freitas, and N. C. M. Gomes, 2016, Jellyfish-associated bacterial communities and bacterioplankton in Indonesian marine lakes: FEMS Microbiology Ecology, v. 92, no. 5, p. fiw064. https://doi.org/10.1093/femsec/fiw064

Cleary, D. F. R., M. R. S. Ferreira, N. K. Bat, A. R. M. Polónia, N. C. M. Gomes, and N. J. de Voogd, 2020, Bacterial composition of sponges, sediment and seawater in enclosed and open marine lakes in Ha Long Bay, Vietnam: Marine Biology Research, v. 16, no. 1, p. 18–31. https://doi.org/10.1080/17451000.2019.1702214

Cleary, D. F. R., Y. M. Huang, A. R. M. Polónia, M. van der Plas, N. C. M. Gomes, and N. J. de Voogd, 2024, Sponges and their prokaryotic com-

munities sampled from a remote karst ecosystem: Marine Biodiversity, v. 54, p. 8. https://doi.org/10.1007/s12526-023-01387-4
Cleary, D. F. R., A. R. M. Polónia, and N. J. de Voogd, 2018, A comparison of prokaryote community composition in two *Cinachyrella* morphospecies and water from West Papuan marine lakes: FEMS Microbiology Ecology, v. 94, no. 2, p. fix175. https://doi.org/10.1093/femsec/fix175
Ferreira, M. R. S., D. F. R. Cleary, F. J. R. C. Coelho, N. C. M. Gomes, Y. M. Huang, A. R. M. Polónia, and N. J. de Voogd, 2020, Geographical location and habitat predict variation in prokaryotic community composition of *Suberites diversicolor*: Annals of Microbiology, v. 70, p. 14. https://doi.org/10.1186/s13213-020-01546-z
Gerovasileiou, V., C. C. Chintiroglou, D. Konstantinou, and E. Voultsiadou, 2016, Sponges as "living hotels" in Mediterranean marine caves: Scientia Marina, v. 80, no. 3, p. 279–289. https://doi.org/10.3989/scimar.04403.14B
Gerovasileiou, V., C. C. Chintiroglou, D. Vafidis, D. Koutsoubas, M. Sini, T. Dailianis, Y. Issaris, E. Akritopoulou, D. Dimarchopoulou, and E. Voultsiadou, 2015, Census of biodiversity in marine caves of the Eastern Mediterranean Sea: Mediterranean Marine Science, v. 16, no. 1, p. 245–265. https://doi.org/10.12681/mms.1069
Gerovasileiou, V., and E. Voultsiadou, 2012, Marine caves of the Mediterranean Sea: a sponge biodiversity reservoir within a biodiversity hotspot: PLoS ONE, v. 7, no. 7, p. e39873. https://doi.org/10.1371/journal.pone.0039873
Giakoumi, S., M. Sini, V. Gerovasileiou, T. Mazor, J. Beher, H. P. Possingham, A. Abdulla, M. E. Çinar, P. Dendrinos, A. C. Gucu, A. A. Karamanlidis, P. Rodic, P. Panayotidis, E. Taskin, A. Jaklin, E. Voultsiadou, C. Webster, A. Zenetos, and S. Katsanevakis, 2013, Ecoregion-based conservation planning in the Mediterranean: dealing with large-scale heterogeneity: PLoS ONE, v. 8, no. 10, p. e76449. https://doi.org/10.1371/journal.pone.0076449
Grottoli, A. G., L. Chapron, D. Gava, and J. W. Olesik, 2020, Natural variability of skeletal elemental phosphorus (P/Ca), lead (Pb/Ca), and barium (Ba/Ca) in the western Pacific sclerosponges *Acanthocheatetes wellsi* and *Astrosclera willeyana*: Geochemistry, Geophysics, Geosystems, v. 21, no. 12, p. e2020GC009245. https://doi.org/10.1029/2020GC009245
Harmelin, J. G., 1997, Diversity of bryozoans in a Mediterranean sublittoral cave with bathyal-like conditions: role of dispersal processes and local factors: Marine Ecology Progress Series, v. 153, p. 139–152. https://doi.org/10.3354/meps153139
Hartman, W. D., 1983, Modern and ancient Sclerospongiae: Notes for a Short Course: Studies in Geology, v. 7, p. 116–129. https://doi.org/10.1017/S0271164800000701
Hartman, W. D., and T. F. Goreau, 1975, A Pacific tabulate sponge, living representative of a new order of sclerosponges: Postilla, v. 167, p. 1–21. https://doi.org/10.5962/bhl.part.6459
Holland, D. C., W. A. Schroder, M. J. Calcott, E. Kaemmerer, V. M. Avery, M. G. Ekins, and A. R. Carroll, 2023, Cyclotheonellazoles D–I, potent elastase inhibitory thiazole-containing cyclic peptides from *Theonella* sp. (2131): Journal of Natural Products, v. 86, no. 9, p. 2216–2227. https://doi.org/10.1021/acs.jnatprod.3c00633
Huang, G. C. L., T. Gray, and D. Bell, 2013, Environmental justice of nuclear waste policy in Taiwan: Taipower, government, and local community: Environment, Development and Sustainability, v. 15, p. 1555–1571. https://doi.org/10.1007/s10668-013-9461-1
Iliffe, T. M., and L. S. Kornicker, 2009, Worldwide diving discoveries of living fossil animals from the depths of anchialine and marine caves: Smithsonian Contributions to the Marine Sciences, v. 38, p. 269–280. https://doi.org/10.5479/si.01960768.38.269
Inoue, S., H. Kayanne, N. Matta, W. S. Chen, and Y. Ikeda, 2011, Holocene uplifted coral reefs in Lanyu and Lutao Islands to the southeast of Taiwan: Coral Reefs, v. 30, p. 581–592. https://doi.org/10.1007/s00338-011-0783-x
Ise, Y., J. Vacelet, M. Mizuyama, and Y. Fujita, 2023, New lithistid sponge of the genus *Sollasipelta* (Porifera, Demospongiae, Tetractinellida, Neopeltidae) from submarine caves of the Ryukyu Islands, southwestern Japan, with redescription of *S. sollasi*: Zootaxa, v. 5285, no. 2, p. 293–310. https://doi.org/10.11646/zootaxa.5285.2.4
Kao, W. H., S. Y. Chang, H. C. Liu, and M. H. Chen, 2007, The mollusks from intertidal and marine shallow water of Lanyu (Orchid Island), Taiwan: Platax, p. 69–92. https://doi.org/10.29926/PLATAX.200712.0007
Karlińska-Batres, K., and G. Wörheide, 2015, Spatial variability of microbial communities of the coralline demosponge *Astrosclera willeyana* across the Indo-Pacific: Aquatic Microbial Ecology, v. 74, p. 143–156. https://doi.org/10.3354/ame01732
Kogawa, M., R. Miyaoka, F. Hemmerling, M. Ando, K. Yura, K. Ide, Y. Nishikawa, M. Hosokawa, Y. Ise, J. K. B. Cahn, K. Takada, S. Matsunaga, T. Mori, J. Piel, and H. Takeyama, 2022, Single-cell metabolite detection and genomics reveals uncultivated talented producer: PNAS Nexus, v. 1, no. 1, p. pgab007. https://doi.org/10.1093/pnasnexus/pgab007
Lang, J. C., W. D. Hartman, and L. S. Land, 1975, Sclerosponges: primary framework constructors on the Jamaican fore-reef: Journal of Marine Research, v. 33, no. 2, p. 223–231.
Lee, S. C., 1980, Intertidal fishes of the rocky pools at Lanyu (Botel Tobago), Taiwan: Bulletin of the Institute of Zoology Academia Sinica, v. 19, p. 1–13.
Lee, S. C., and C. H. Lee, 1981, A collection of subtidal fishes from Lanyu (Botel Tobago), Taiwan with a note on a newly recorded serranid, *Ypsigramma lineata*: Bulletin of the Institute of Zoology Academia Sinica, v. 20, p. 87–89.
Macartney, K. J., M. S. Pankey, M. Slattery, and M. P. Lesser, 2020, Trophodynamics of the sclerosponge *Ceratoporella nicholsoni* along a shallow to mesophotic depth gradient: Coral Reefs, v. 39, no. 6, p. 1829–1839. https://doi.org/10.1007/s00338-020-02008-3
Maldonado, M., 2016, Sponge waste that fuels marine oligotrophic food webs: a re-assessment of its origin and nature: Marine Ecology, v. 37, no. 3, p. 477–491. https://doi.org/10.1111/maec.12256
Manconi, R., and A. Serusi, 2008, Rare sponges from marine caves: discovery of *Neophrissospongia nana* nov. sp. (Demospongiae, Corallistidae) from Sardinia with an annotated checklist of Mediterranean lithistids: ZooKeys, v. 4, no. 4, p. 71–87. https://doi.org/10.3897/zookeys.4.39
Mayer, D., Z. Dubinsky, and D. Iluz, 2016, Light as a limiting factor for epilithic algae in the supralittoral zone of littoral caves: Frontiers in Marine Science, v. 3, p. 18. https://doi.org/10.3389/fmars.2016.00018
Meroz-Fine, E., S. Shefer, and M. Ilan, 2005, Changes in morphology and physiology of an East Mediterranean sponge in different habitats: Marine Biology, v. 147, p. 243–250. https://doi.org/10.1007/s00227-004-1532-2
Montefalcone, M., G. De Falco, E. Nepote, M. Canessa, M. Bertolino, G. Bavestrello, C. Morri, and C. N. Bianchi, 2018, Thirty year ecosystem trajectories in a submerged marine cave under changing pressure regime: Marine Environmental Research, v. 137, p. 98–110. https://doi.org/10.1016/j.marenvres.2018.02.022
Nepote, E., C. N. Bianchi, C. Morri, M. Ferrari, and M. Montefalcone, 2017, Impact of a harbour construction on the benthic community of two shallow marine caves: Marine Pollution Bulletin, v. 114, no. 1, p. 35–45. https://doi.org/10.1016/j.marpolbul.2016.08.006
Ogawa, K., H. Yokochi, and K. Matsuzaki, 1993, Taxonomical and ecological notes on the sclerosponges newly found at Amitory Bay, Iriomote Island, Okinawa, Japan: Nankiseibutu, The Nanki Biological Society, v. 35, no. 1, p. 33–38.
Paskoff, R. P., 2005, Karst coasts: In: Schwartz, M. L. (ed.), Encyclopedia of Coastal Science, Encyclopedia of Earth Science Series, p. 581–586. Springer, Dordrecht. https://doi.org/10.1007/1-4020-3880-1_187
Pisera, A., and V. Gerovasileiou, 2021, Lithistid demosponges of deep-water origin in marine caves of the north-eastern Mediterranean Sea:

Frontiers in Marine Science, v. 8, p. 630900. https://doi.org/10.3389/fmars.2021.630900
Please add Pulitzer-Finali, G. (1993). A collection of marine sponges from East Africa. Annales Museo Civico Storia Naturale “Giacomo Doria”. 89: 247-350.
Quinn, N. J., and B. L. Kojis, 1999, Community structure of the living fossil coralline sponge populations at the Grotto, Saipan, Northern Mariana Islands: Bulletin of Marine Science, v. 65, no. 10, p. 227–234.
Radolović, M., T. Bakran-Petricioli, D. Petricioli, M. Surić, and D. Perica, 2015, Biological response to geochemical and hydrological processes in a shallow submarine cave: Mediterranean Marine Science, v. 16, no. 2, p. 305–324. https://doi.org/10.12681/mms.1146
Reigle, N. J., 1963, Notes on the mollusks of Lanyu, Taiwan: Quarterly Journal of the Taiwan Museum, v. 16, p. 81–87.
Schuster, A., A. Pisera, M. Ekins, and C. Debitus, 2021, New genus and species of lithistid demosponges from submarine caves in Nuku Hiva (Marquesas Islands) and Tahiti Iti (Society Islands), French Polynesia: The European Zoological Journal, v. 88, no. 1, p. 749–770. https://doi.org/10.1080/24750263.2021.1939450
Schuster, A., A. Pisera, M. Kelly, L. J. Bell, S. A. Pomponi, G. Wörheide, and D. Erpenbeck, 2018, New species and a molecular dating analysis of *Vetulina* Schmidt, 1879 (Porifera: Demospongiae: Sphaerocladina) reveal an ancient relict fauna with Tethys origin: Zoological Journal of the Linnean Society, v. 184, no. 3, p. 585–604. https://doi.org/10.1093/zoolinnean/zlx114
Sket, B., 1996, The ecology of anchialine caves: Trends in Ecology and Evolution, v. 11, no. 5, p. 221–225. https://doi.org/10.1016/0169-5347(96)20031-X
Slattery, M., D. J. Gochfeld, C. G. Easson, and L. R. K. O’Donahue, 2013, Facilitation of coral reef biodiversity and health by cave sponge communities: Marine Ecology Progress Series, v. 476, p. 71–86. https://doi.org/10.3354/meps10139
Tzabari, M., D. Mayer Mayron, D. Iluz, Z. Dubinsky, and C. Haspel, 2018, Linear polarization characteristics within the Rosh HaNikra mid-littoral cave, Israel: Frontiers in Marine Science, v. 5, p. 192. https://doi.org/10.3389/fmars.2018.00192
Vacelet, J., 1985, Coralline sponges and the evolution of Porifera: In: S. Conway Morris, J. D. George, R. Gibson, and H. M. Platt (eds.), The Origins and Relationships of Lower Invertebrates, Clarendon Press, Oxford, p. 1–13.
Vacelet, J., N. Boury-Esnault, and J. G. Harmelin, 1994, Hexactinellid cave, a unique deep-sea habitat in the scuba zone: Deep Sea Research Part I: Oceanographic Research Papers, v. 41, no. 7, p. 965–973. https://doi.org/10.1016/0967-0637(94)90013-2
Vacelet, J., 1996, Deep-sea sponges in a Mediterranean cave: In: Ott, J., and M. Stachowitz (eds), Deep-sea and extreme shallow-water habitats: affinities and adaptations, Biosystematics and Ecology Series, v. 11, p. 299–312.
van Hengstum, P. J., J. N. Cresswell, G. A. Milne, and T. M. Iliffe, 2019, Development of anchialine cave habitats and karst subterranean estuaries since the last ice age: Scientific Reports, v. 9, p. 11907. https://doi.org/10.1038/s41598-019-48058-8
Willenz, P., and W. D. Hartman, 1989, Micromorphology and ultrastructure of Caribbean sclerosponges: Marine Biology, v. 103, p. 387–401. https://doi.org/10.1007/BF00397274
Yu, H. P., 1985, Notes on the land hermit crabs (Crustacea, Decapoda, Coenobitidae) from Lan-yu Island in the southern Taiwan: Journal of Taiwan Museum, v. 38, p. 59–64.