# LIFE IN EXTREME OCEAN ENVIRONMENTS: ANCHIALINE CAVES

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## Contents



## Summary

Anchialine habitats are flooded inland marine caves and smaller voids that lack any direct connection with the sea. They fall well within the ecological definition of extreme environments since production is severely reduced due to environmental conditions: there is no light (and no photosynthesis), and the groundwater column is extremely stable, preventing any large scale injection of external organic matter into the system. In addition, a non-negligible fraction of the energy sustaining the food web is derived from chemoautotrophic microorganisms that take advantage of the sharp redox interfaces in the cave water column, to reduce inorganic carbon using compounds such as sulfides or ammonium as electron donors. Most anchialine animals are of undeniable marine origin and are commonly blind and unpigmented, these features being shared with ordinary subterranean animals. Many represent long term survivors of ancient lineages, and display extremely disjunct and localized distributions, probably modulated by vicariance via plate tectonics. This disproportionate representation of phylogenetically ancient taxa compared to the rest of the marine realm may well depend on the large scale historical and spatial continuity of the extended network of flooded fissures, cracks and caves constituting the anchialine environment, and also on the high environmental buffering effect of the network. This anchialine network must have persisted since the appearance of emerged land on Earth, irrespective of the

displacement of coastlines. A few anchialine animals appear related to deep-sea forms, suggesting a deep-sea origin for a small fraction of the cave fauna. However, recent phylogenetic analyses point to a shallow water origin for the majority of anchialine animals. Numerous new species, genera, families and even a new class of crustaceans have been described from anchialine caves. This degree of novelty makes anchialine habitats uniquely important but the restricted distribution and isolation of such species, often to a single cave system on a single island, also renders them extremely vulnerable to the unsustainable levels of development for tourism that are threatening these coastal habitats.

## 1. Introduction

Terrestrial habitats are classified as extreme or stressful according to traditional ecological criteria, foremost of which is the emphasis on their very limited production due to physical constraints, such as cold at high latitudes or aridity in desert areas. In the sea, however, the label "extreme" is frequently applied according to less strict criteria. Deep-sea hydrothermal vents are, for example, intuitively considered as extreme habitats, and there is an agreement that the geochemical conditions impose severe physiological demands on their inhabitants. But life is surprisingly plentiful at vents and vent dwellers show rapid growth in spite of the apparent severity of the environment. Other types of marine habitat fall better within the more ecological definition of extreme environments. These are the abyssal plains, hadal trenches, plus a special type of subterranean environment in the littoral zone that will be considered herein: anchialine caves (see Figure 1).

Figure 1. Recent developments of cave-diving techniques have enabled the exploration of the anchialine environment, a cryptic marine habitat in the littoral zone. Survey of a flooded breakdown room in *Cova de sa Gleda*, Mallorca, Balearic Islands. *[Photo © O. Espinasa]*

All these habitats share a restrictive set of environmental conditions, namely extreme oligotrophy, environmental stability and complete and permanent darkness. These three features in common underlie the recognition of numerous parallels between life in caves and life in the deep sea.

## 2. The anchialine environment: a subterranean marine/freshwater ecotone

Anchialine habitats are water-filled inland voids that display obvious marine influences (see Figure 2). The marine ties are manifested in the major ionic composition of the water, with a prevalence of $Cl^-$ and $Na^+$ ions, or raised concentrations of both compared to those of ordinary continental waters. In addition, the anchialine groundwater table oscillates with the outside marine tides, although this oscillation is somewhat buffered in amplitude and propagated with a time lag.

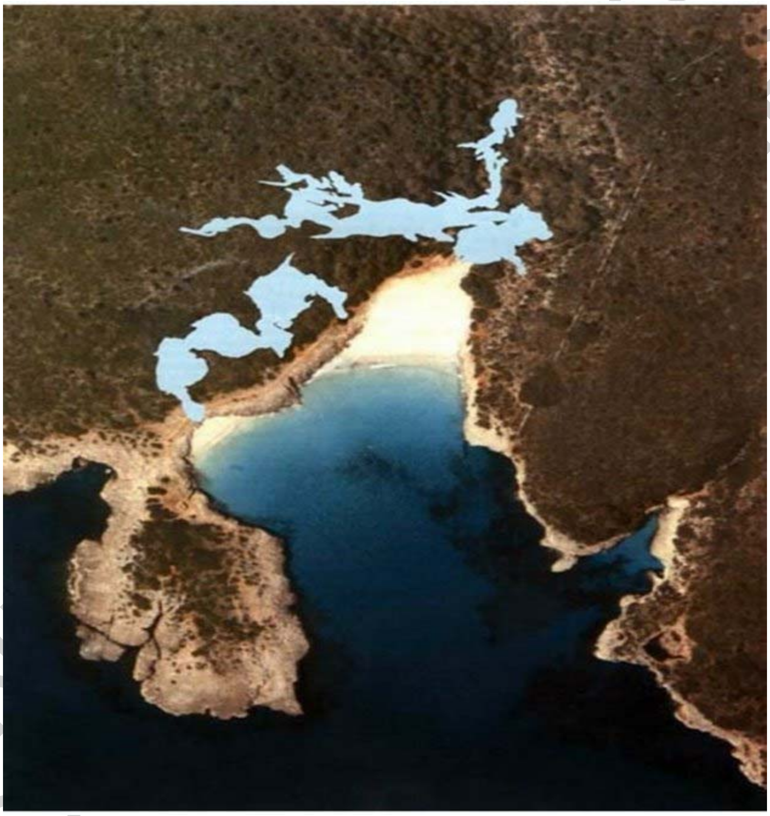

Figure 2. Extension of the subterranean anchialine system at *Cala Varques*, Mallorca.

These groundwater masses should have their connection to the open sea filtered by percolation through bedrock in order to be considered anchialine proper. Otherwise they should be classified as ordinary submarine or littoral caves. The restricted communication with the sea outside and the atmosphere impedes wind- and wave-induced mixing, which leads to the establishment of a highly stratified water column (Figure 8). The surface layers are more or less diluted by infiltration of fresh water, forming a fresh or brackish water lens that overlies the major volume of denser, full-strength seawater. The shape and thickness of this lens is determined by the interplay of the so-called Ghyben-Herzberg principle, the transmissivity of the bedrock and the rainfall balance. The transition zone between the fresh and the marine water, the so-called halocline, is produced by mixing at the interface between the two water bodies. Cave divers know it well since this is the region where vision turns fuzzy due to the unstable optical properties of the water. The thickness of the halocline diminishes progressively in caves located further inland from the coast owing to the increased dampening of tidal oscillations and consequent reduction of tidal mixing.

In caves excavated in calcareous bedrock—the majority of anchialine caves known thus far—the combination of stagnation and high content of calcium and bicarbonate ions in the fresh groundwater creates a peculiar geo-chemical environment in the upper parts of the water column. Due to the unimpeded diffusion of carbon dioxide towards the cave atmosphere, the surface layers become over-saturated in $Ca^{2+}$, and the consequent chemical readjustments lead to the precipitation of calcium carbonate. The air-water interface becomes covered with calcite rafts somewhat reminiscent of marine ice fields. This calcite (or aragonite) also precipitates forming overgrowths around the flooded stalactites and stalagmites, which after that attain a characteristic pear-shaped outline, or along the rim of the cave lake forming a narrow band similar to a Mediterranean *trottoir* (Figure 3). The thickness of this horizontal band is roughly coincident with the maximum amplitude of the water-level oscillation in the cave, and it is interesting to note here that the record of horizontal bands preserved in the walls and ceilings of coastal caves represents an invaluable tool for the study of past sea-level oscillations (Figures 3 and 5).

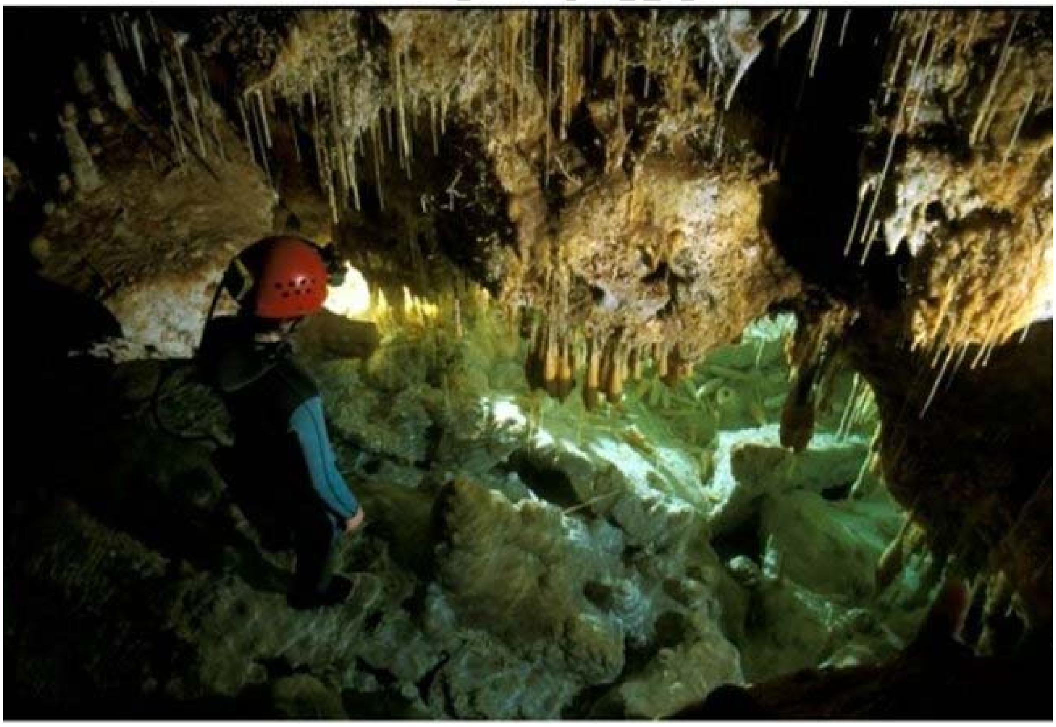

Figure 3. A typical anchialine landscape in *Cova des Pas de Vallgornera*, Mallorca. Notice the band of pear-shaped stalactites recording past glacial sea-level oscillations. These types of speleothems are typically developed in anchialine caves. *[Photo © A. Merino]*

Typical anchialine and submarine or littoral caves differ markedly in the structure of the water column in the cave lake but any classification of natural phenomena involves a degree of over-simplification, and intermediates between these two types of caves are known. Indeed, different parts of the same flooded cave system can be under different regimes, anchialine or ordinary marine, mostly depending on the cave topography. A useful clue serving to distinguish between these two types of cave at a glance, is the absence of sessile filter-feeders in the former. The stagnant water regime fails to provide a living for these animals, that are so common in submarine tunnels or caves scoured by strong currents.

## 3. The marine condition of anchialine caves

The inclusion of the anchialine environment within the marine realm is debatable. There are many anchialine caves with very low salinity parts, and others are located several kilometres inland from the coast. The term anchialine is derived from the Greek *anchialos* meaning “close to the sea”.

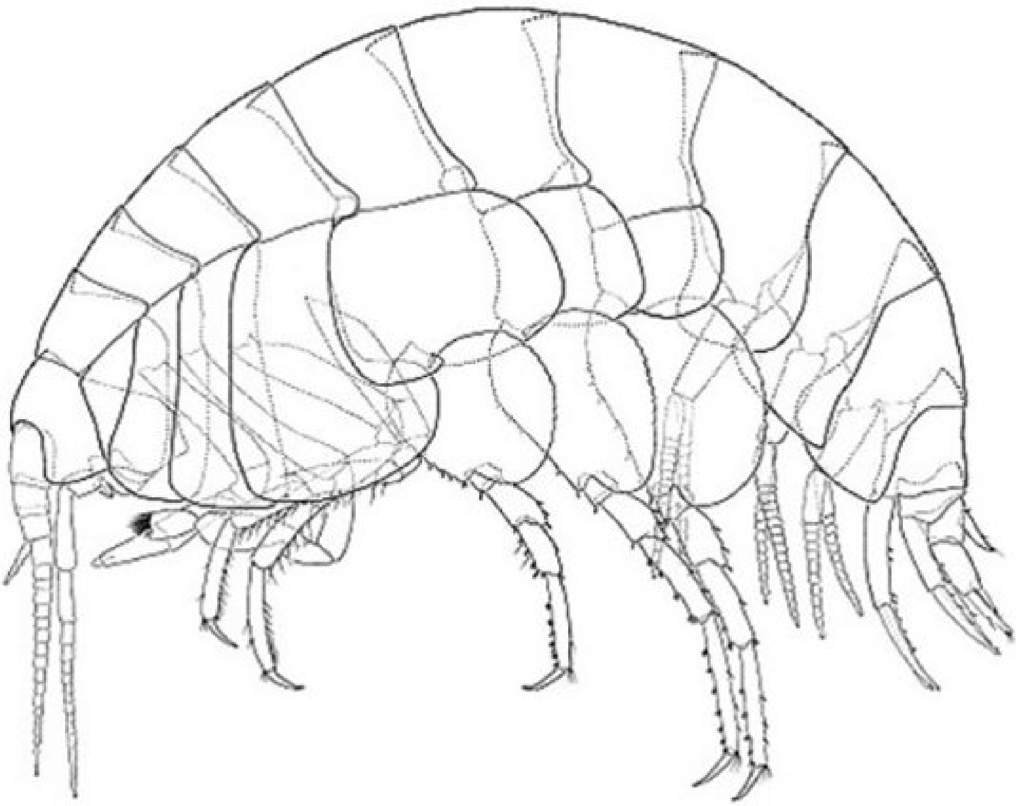

Figure 4. *Ottenwalderia kymbalion*, the only representative of the marine crustacean amphipod family Lysianassidae known to have penetrated into inland waters, from the freshwater reaches of anchialine caves in the Dominican Republic. The marine condition of anchialine caves is clear from their faunal assemblages, since virtually all their members have a traceable direct marine origin.

There are few doubts, however, from a zoological standpoint, that anchialine caves belong to the marine realm. Using the Crustacea as a reference group—they are the predominant metazoans in subterranean waters—limnologists will hardly find in the anchialine environment any representatives of the higher rank taxa that characterize the plankton and benthos of continental waters. Thus, there are no branchiopods (water-fleas) nor syncarids, and the copepods do not belong to the typically freshwater groups (i.e. Diaptomidae, Cyclopinae, Eucyclopinae). There is virtually no representation of the typical fresh groundwater amphipod families (Crangonyctidae, Niphargidae), and the same holds for the isopods, with absence of Asellidae and Stenasellidae. Marine zoologists feel comfortable working in anchialine systems, with almost every taxon found having a traceable marine origin, even those inhabiting the lower salinity reaches of the cave system (see Figure 4).

## 4. Typology and distribution of anchialine environments

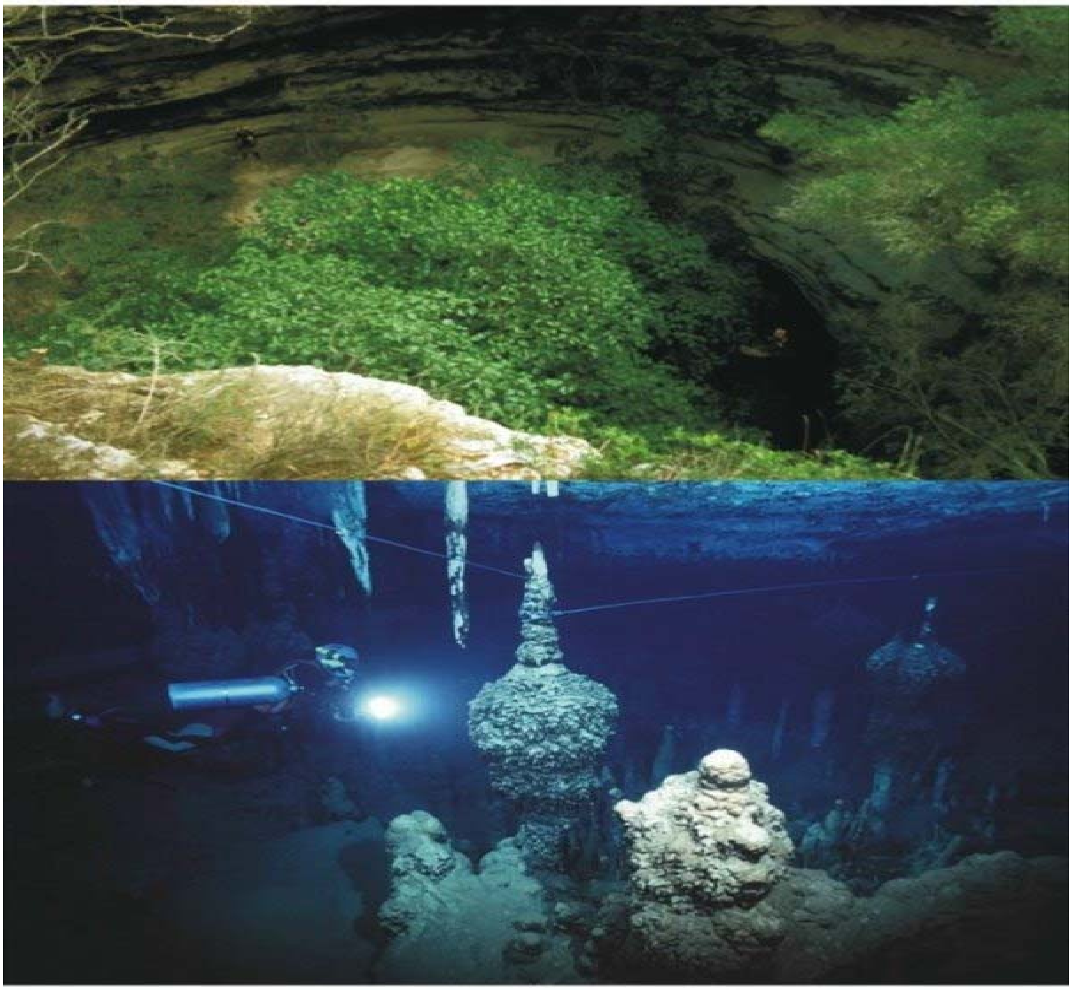

Figure. 5. The more common types of anchialine environments. Cenote-type entrance at *Cova de sa Gleda*, a partially-flooded collapse cave on Mallorca. This kind of caves is originated by breakdown undermining of preceding karstic chambers after the periodic loss of the groundwater's buoyant support during low glacial sea stands. Notice the thickened band on the drowned stalagmites recording a past sea-level stand. *[Photo © A. Merino and O. Espinasa, respectively]*

Anchialine waters are usually found in flooded karstic caverns excavated in coastal carbonate outcrops (see Figure 5). These caves were invaded by the sea after marine transgressions and/or drowning of the coast. This is demonstrated by the presence of stalactites and stalagmites—speleothems formed only under subaerial conditions—in the flooded chambers of the caves.But many can be phreatic in origin: the aggressive dissolving power of the groundwater of the marine/freshwater mixing zone contributes to the formation and eventual widening of the karstic voids.

In addition, a few anchialine caves are geologically very different in origin, arising as flooded volcanic lava tubes on oceanic islands such as the Galapagos, Canaries, Western Samoa and Hawaii (Figure 6). Caves and lava tubes represent the most easily accessible of anchialine habitats, but most of the anchialine water in coastal aquifers remains inaccessible to man because it lies in small rock fissures and voids. These waters can be eventually accessed via artificial wells and boreholes which provide sampling opportunities for the researcher. Anchialine waters can also be found in flooded tectonic cracks in coastal cliffs, or in the so-called anchialine pools—open depressions separated from the sea by bars of volcanic debris or coral rubble where the groundwater appears (Figure 7).

Figure 6. The more common types of anchialine environments. *Jameo de los Siete Lagos*, a partially flooded lava tube on Lanzarote (Canary Islands). Notice the record of the tidal oscillation on the walls.

Figure 7. The more common types of anchialine environments. Anchialine pool on loose volcanic debris on Lanzarote; notice the dried algae on the rims recording the height of the tidal oscillation.

Anchialine environments do not develop wherever appropriate coastal rock outcrops occur. They are absent from broad stretches of coastline that at first glance appear suitable, for example the Basque or Welsh coasts on the European Atlantic shore. The anchialine world appears confined to tropical latitudes, with a few sub-tropical outliers scattered over the northern Hemisphere (e.g. Bermuda and the Canaries in the Atlantic, several sites in the Mediterranean, and the Ryu-Kyu Archipelago in the north-west Pacific). Caves along the Croatian coast of the Adriatic Sea (at 45ºN) are the most northerly anchialine sites known, and caves in *Île des Pins* (New Caledonia, at 22ºS) are their southernmost counterparts.

It seems likely that this circum-tropical distribution pattern results from the interaction of a number of causal factors. Thus, the development of an anchialine regime relies on the intrusion of marine water into coastal aquifers, and this depends on the hydraulic conductivity of the bedrock, among other variables. Raised coral-reef terraces, especially those of recent (upper-Tertiary to Quaternary) origin that are not diagenetically mature, have a high porosity and are thus more prone to be affected by generalised marine intrusion than outcrops of (older) dense crystalline carbonates. The latter are almost impermeable, and marine water can only intrude following fissures and/or previously excavated karstic conduits. Consequently there is a lower chance for the establishment of an anchialine regime in crystalline outcrops, since flooded caves in such areas generally remain well-connected to the sea.The intrusion of the marine wedge into the coastal aquifers also depends on regional pluviometry. Aquifers in arid or semi-arid land are in general more prone to suffer intrusion than those placed in rainy regions, where fresh groundwater flowing to the sea impedes the penetration of marine waters. Likewise one might expect an over-representation of anchialine environments on islands given that the ratio between the surface (to collect rainfall) and the coastline perimeter is proportionately lower than in continental regions.

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**Biographical Sketches**

**Damià Jaume** received his Ph.D. in Ecology at the University of Barcelona in 1994 with a thesis dealing with the ecology and biogeography of planktonic crustaceans of the Spanish reservoirs. He then moved to the Department of Zoology of The Natural History Museum, London, where he specialized in Systematics and Biogeography of copepod crustaceans under the supervision of Prof. G.A. Boxshall. Currently he is Research Scientist at the Natural Resources department of IMEDEA, a joint research institute between the Spanish Scientific Research Council (CSIC) and the University of the Balearic Islands, based in Mallorca. His current research topics cover the systematics and historical biogeography of inland groundwater crustaceans, especially those of thalassoid origin, plus all aspects concerning life in anchialine caves. In addition he maintains an active research interest in the systematics and biogeography of bathyal amphipods from the Atlanto-Mediterranean region. He has published about 60 scientific papers, most dealing with the description of new crustacean taxa exhibiting extreme disjunct and relict distributions from anchialine cave waters worldwide. His usual research playground consists of sea-water flooded caverns located beneath the most popular island holiday destinations of the world, in the Mediterranean and the West Indies.

**Geoff Boxshall FRS** has been a researcher at the Natural History Museum, London since completing his PhD in 1974. His research has focused on the systematics, functional morphology and evolution of copepods and related crustaceans, extending across the whole range of life styles from parasites to plankton. He has specialised in research on the biology and control of sealice, a major health problem for salmonid aquaculture, and in phylogenetic studies of copepods, especially those from anchialine habitats. His research has been recognized in a series of awards: Scientific Medal of the Zoological Society of London for outstanding contribution to Zoology by a scientist under 40 (in 1986), elected Fellow of The Royal Society (in 1994), and Excellence in Research Award, The Crustacean Society (in 1998). He has published extensively; including over 130 scientific papers and has co-authored several books including *Copepod Evolution* (1991), *Dictionary of Ecology, Evolution and Systematics* (2$^{nd}$ edition, 1998), and *The Cambridge Illustrated Dictionary of Natural History* (1987). He has served on numerous scientific committees and editorial boards, and he is currently the President of the World Association of Copepodologists.